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A STUDY OF ASPECTS OF THE NUTRIENT CYCLE IN A NEW SOUTH WALES CONIFER FOREST

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This is to certify that, apart from the exceptions below, the work presented in this thesis is my own. Exceptions include assistance recorded in the acknowledgements and the data in Chapter five on the forest floors of the species other than Pinus nigra var. maritima. These data were used for comparative purposes through the permission of Dr. M.T. Tanton, of the Department of Forestry, Australian National University.

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INTRODUCTION

In the temperate regions of Australia large areas of indigenous forest and grassland are being converted to the growing of exotic Coniferae. Given the current demand for building timber, wood chips, pulp and other softwood derived products, this conversion is likely to continue at an increasing rate for some time into the future.

In the South-Eastern part of Australia one species, Pinus radiata D. Don, is being planted to the virtual exclusion of all others. The only notable exception being Pseudotsuga menziesii (Mirbel). Reasons for the widespread growth of P. radiata include its high growth rate and the current lack of any significant plant parasite or pathogen except, in certain areas, an introduced wood wasp Sirex noctilio (Hymenoptera: Siricidae).

It is considered that undue reliance is being placed on this one tree species. Plant parasitic arthropods and fungal pathogens are potentially dangerous where large areas of monospecies plantations are being created, as is occuring at present. One illustration of the dangers of this type of situation is already available from New Zealand where the larva of Selidosema suavis Butl. (Lepidoptera: Geometridae) has adapted to feeding on the foliage of P. radiata and epizootics of irregular occurrence have been recorded which defoliated considerable areas of commercial forests. A similar situation could well arise in Australia either through adaptation of a

local species or failure in quarantine procedures.

It is also felt that, in comparison with other types of agriculture, plantation forestry as practised in Australia tends to be exploitive. Inimical effects on several properties of forest soils that evolved under indigenous broadleaf vegetation have been recorded and may prove significant over the course of a number of rotations. Apart from this, a crop of one tree species follows immediately after the previous in most situations and on some low quality soils growth rates in subsequent crops have become depressed requiring fertilization for their improvement. This latter practice may be expected to become a regular feature of commercial forestry as may certain of those prevalent in other branches of agriculture. These include the interspersion of soil ameliorating crops between those of conifers, 'nurse' crops of legumes and the application of growth active compounds.

It is considered that the current exploitive practices are likely to continue for some years to come. However, it is to be hoped that, in the future, a philosophy of commercial forestry as a more exact and conservationist discipline will develop. Hopefully, this will be based on a systems concept which may help to ensure that sustained yield management policies are initiated. These policies should be aimed at the prevention of net losses of plant nutrient elements from forest areas and the preservation of a favourable physical soil status.

To make a comparative study of aspects of the internal nutrient cycles in several conifer species, the work

presented here was designed to fall into three parts. The first is a comparative study of the magnitude of litterfall accession and selected of its constituent plant nutrient chemicals in four species of Coniferae viz. Pinus lambertiana Douglas, Pinus nigra Arnold var. maritima (Aiton), Pinus ponderosa Douglas and Pseudotsuga menziesii (Mirbel). Also included is an investigation of the spatial disposition of the material accessed.

The second part of the work is an assessment of the magnitude and seasonal variation of the organic matter of the forest floor in a Pinus nigra var. maritima stand. These characters are compared with like data obtained from sampling the forest floors of several other closed canopy conifer stands growing in the same locality.

A study of the litter animal community in the P. nigra stand and of its reaction to DDT and carbaryl comprises the final part of the work.

STUDY AREA

The study area is located in Bago State Forest (New South Wales Forestry Commission No. 560) in the Southern Tablelands of New South Wales. This region was chosen because the cool temperate climate ressembles that in which conifers are widely grown in other parts of the world. Other features of the area are a moderate rainfall and a considerable local investment in forestry.

Bago Forest was chosen because it possesses a range of stands of similar age growing in a relatively

homogeneous area. These stands were near maturity and provided a continuous and well developed forest floor thereby reducing sample variance to a minimum.

Bago Forest is located on the Bago Plateau. This is an undulating area which extends approximately 32km. southwards from Batlow (35°31'S., 148°10'E.) with a width varying between 11 and 24km. The plateau rises from 920 to 1460m. although the study area was at an altitude of approximately 1000m.

The geology of the area is simple. Underlying rocks consist of granite, mainly granodiorite, although tertiary basalt flows are scattered through the plateau (Cooper, 1966). Other rocks occur but in the study locality were uniformly granitic in nature.

CLIMATE

A temperature and precipitation recording station was located approximately 1.5km. from the study plots. Although some 60m. higher, conditions measured were probably comparable to those pertaining in the plots. Mean precipitation is 142cm. as measured over the 27 year period prior to 1966. Most of this falls as winter snow (Plate 2) although minor precipitation peaks also occur in summer and spring (Cooper, 1966).

Mean monthly maximum temperatures range from a high of 23.4°C. in February to a low of 6.35°C. in June, as measured over the 14 year period prior to 1965. For the same term, mean monthly minima varied from -1.06°C. in

Plate 1: Pinus nigra var. maritima stand, Cpt. 53, Bago State Forest where much of the experimental work was carried out.

Plate 2: Pinus nigra var. maritima stand, Cpt. 53, Bago State Forest. Winter aspect of forest floor.

June to 10.12°C. in February.

The predominant anticyclonic weather patterns of the region give rise to a climate dominated by westerly air streams although northerly air influences occasionally contribute to the general weather pattern (Cooper, 1966).

STUDY PLOTS

Plots were laid out in near mature, closed canopy stands of Pinus lambertiana Douglas (Cpt. 17), Pinus nigra Arnold var. maritima (Aiton) (Cpt. 53), Pinus ponderosa Douglas (Cpt. 33) and Pseudotsuga menziesii (Mirbel) (Cpt. 9) located at approximately 35°35'S., 148°06'E. and at an altitude varying from 950m. to 1100m. In addition, smaller plots in the P. nigra stand were set out within the larger plots described above for the litter and faunal studies reported in Chapters five and six.

All plots were one hectare in area and square in shape except for that in the Ps. menziesii stand which was rectangular due to limitations imposed by stand shape. The smaller plots in the P. nigra stand were sited within the hectare plot and are described in Chapter five.

Individual locations were chosen on the basis of their approximate comparability with respect to soils, exposure, slope, drainage and physical proximity to the other sites in the study. Placement of plots within stands was decided on the basis of completeness of canopy cover and continuity of the litter layers. Stand edges and other atypical sampling situations were avoided.

Plate 3: Pinus lambertiana stand, Cpt. 17, Bago State Forest. Callus growth on cut stump. Ruler is 0.38 m.

Plate 4: Pinus nigra var. maritima stand, Cpt. 54, Bago State Forest. Mound of Coptotermes lacteus (Froggatt) on dead eucalypt log. Ruler is 0.38 m.

Plate 5: Eucalypt stump cut to show perched litter and central pipe. Cpt. 9, Bago State Forest.

Plate 6: Wombat (Vombatus ursinus) hole in Pinus ponderosa stand. Cpt. 33, Bago State Forest. Ruler is 0.38 m.

TABLE 1. Stand histories and assessment data.

Species	Year of Planting	Stocking Rate (trees/ha)	Basal area (sq.m/ha)	Mean Heights (metres) & 95% Confidence Limits	Mean d.b.h. in metres & 95% Confidence Limits
P. lambertiana	1929	692	94.043	24.536 (24.076-24.978)	0.405 (0.383-0.427)
P. nigra var. maritima	1934	1013	64.325	20.147 (19.660-20.666)	0.279 (0.262-0.296)
P. ponderosa	1933	848	75.896	19.842 (18.928-20.726)	0.331 (0.309-0.353)
Ps. menziesii	1927	1462	73.23	23.765 (22.921-24.606)	0.244 (0.234-0.255)

The histories of the stands in which the plots are located uniformly include clear felling and burning of the indigenous vegetation, planting of the conifer crop, release cutting of unwanted vegetation, pruning and thinning (unpublished Compartment Histories, N.S.W. Forestry Commission). Stand planting dates and assessment data current for the time of the experiments are presented in Table one.

In all plots, litter layers were continuous (Plate 1) and ground vegetation virtually limited to a few individuals of Pteridium esculentum (Forst. f.). A notable feature of the forest floor is the presence of calluses on the cut stumps of trees removed some years previously during thinning operations (Plate 3). This was particularly obvious in the P. lambertiana and P. nigra stands suggesting the occurrence of copious root grafting in these species.

Some features of the forest floor, possibly peculiar to the Australian environment, include considerable amounts of undecomposed slash from pruning and, notably, dead logs of the indigenous vegetation felled previous to planting the conifer crop (Plates 1 and 2). Associated with a few of the dead eucalypt logs are the large mounds of Coptotermes lacteus (Froggatt) (Isoptera: Rhinotermitidae) (Plate 4). On many logs and stumps, perched litters and rudimentary "soils" form. This is illustrated in Plate 5 where the saw cuts also expose a central pipe in the stump, originally caused in the living tree by Porotermes adamsoni (Froggatt) (Isoptera: Termopsidae). Wombats

(Vombatus ursinus (Shaw, 1800)) are not uncommon in conifer plantations and their large holes and scrapings in the litter are obvious features of the forest floor in many areas (Plate 6).

CHAPTER ONE

METHODS

In general, methods relevant to a particular chapter are described therein. Certain techniques common to more than one, are described below.

DATA HANDLING

During collection, data were entered on coding forms in a pre-defined format and as soon as practicable, punched on computer data cards. Magnetic tape was employed for long term storage of most data with the cards being retained as a "back up".

There were two principal reasons for this. Firstly, all data were duplicated shortly after collection reducing the possibility of their loss. The likelihood of this occuring was further reduced by separate storage of the magnetic tape and cards. The second reason was to permit summary of data soon after collection allowing a ready interim check on sample means, variances and other statistics.

The computation of results from instrument output during chemical analysis posed a different problem. The use of a quadratic model for the calibration of the various analytical instruments entailed considerable computation and a computer program was written to handle this.

This program is described in the Appendix.

DATA STRUCTURES AND STATISTICAL METHODS

Much of the data presented in this thesis is multivariate in nature. That is, several characteristics of each sampling unit are measured and considered as independent descriptions. These characteristics, known statistically as variables, may be of differing types: some chemical, some physical. Examples of variables used to describe individual sampling units in the present study included concentrations of several plant nutrient elements, weights of various components and numbers of selected animal taxa.

Multivariate data may be dismembered and the constituent variables analysed independently of one another. However, this process entails a loss of information and when the number of variables become large and their interrelationships complex, it is preferable to examine them simultaneously to obtain an holistic approach to the problems of comparison or association. This does not imply denigration of the analysis of invidual variables since the information obtained may be regarded as complementary to that gained from the multivariate approach. It is, however, often difficult to effectively resynthesise a conceptual whole from the results of multiple univariate analyses considered in isolation.

MULTIVARIATE METHODS

The multivariate methods used in this thesis fall into two groups. The first comprises two methods of comparing samples, or groups of samples; canonical variate analysis and a simultaneous test procedure multivariate analysis of variance. The second group contains two methods providing measures of association. The first, canonical correlation analysis, assesses the degree of association between two sets of variables. The second method, multiple regression analysis, relates a dependent to an indefinite number of independent variables.

Canonical variate analysis (CVA) allows examination of sample interrelationships in a number of dimensions that may be substantially less than that of the original test space. In this method, the data are transformed to a number of orthogonal linear combinations of the original variables chosen to maximise sample differences. Individual samples are assigned a score on the basis of these linear combinations and are plotted on orthogonal axes in the reduced space. These axes are orientated in the direction of greatest variability with each sequential axis accounting for a maximal portion of the remaining variance. It is considered that in the practical application of this technique, eigenvalues exhibiting small proportions of total variance will add little to the resolution of sample relationships (see also Buzas, 1967), although adjudged significantly different from zero using Bartlett's test.

Thus, axes accounting for less than an arbitrary value of less than five per cent. of total variability are not considered further. Those retained are denoted "useful". The advantages of graphical expression and transformation to orthogonal variables are discussed by Tukey and Wilk (1966).

CVA also provides information on the discriminating power of the individual variables. This may allow greater economy of sampling effort in the comparison of related statistical universes by permitting deletion of variables with constantly low discriminating power. A drawback of the method is that it allows no exact test of the significance of sample differences and the canonical axes may be difficult to interpret (Finney, 1956). However, this may not be a problem where the aim is to establish the relationships between samples and not attempt to explain them in terms of factors external to the analysis.

CVA has been used to resolve sample differences in a number of ecological and taxonomic situations. Some examples of its ecological use include the comparison of faunal areas (Buzas, 1967), geographic variants of animal species (Seal, 1964), ground flora of some English beechwoods (Norris and Barkham, 1970) and microtopographic variation in selected chemical attributes of gilgaied soils (Horton et al., 1968).

A simultaneous test procedure in multivariate analysis of variance (STP), based on Roy's maximum characteristic root procedure, has been advanced by Gabriel (1968) as a substitute for CVA. However, it appears that the two

methods are at least partly complementary in that CVA allows graphical expression of pattern in the simpler situation of orthogonality and reduced dimensionality. In contrast, STP analyses resolve fine sample detail in the more immediately meaningful terms of individual variables taken either singly or simultaneously. This latter form of analysis also provides exact tests of the significance of sample differences at any required probability level.

Canonical correlation analysis is a procedure which assesses the intercorrelations between two sets of variables by computing the maximum correlation (canonical correlation) between successive orthogonal linear combinations of the two sets. There may be a number of such orthogonal pairs of canonical correlations, each being chosen to maximise the correlation between the two sets of variables known respectively as predictors and criteria. These terms bear no connotation of dependence or independence. The significance of each canonical correlation may be tested by the distribution of Λ, a quantity which is distributed approximately as chi-square and is defined (Cooley and Lohnes, 1962) as:

$$\Lambda = \prod_{i=r+1}^{p_2} (1-\lambda_i)$$

where p_1 is the number of variables in the smaller set

p_2 is the number of variables in the larger set

r is the number of eigenvalues removed

$(p_1-r)(p_2-r)$ are the degrees of freedom of Λ

This technique has been little used in the biological

sciences, one of the few examples being that of Cassie and Michael (1968) in a study of the association between fauna and sediment size in an intertidal mudflat.

Multiple regression is a well known technique long used to assess the association between a dependent and a number of independent variables. The form used in the analyses presented in Chapter four is known as stepwise multiple regression in which the independent variables are entered into the regression equation in decreasing order of their correlation with the dependent variable. The various forms of this analysis are discussed by Snedecor and Cochran (1967).

COMPUTATION

The statistical analytical results presented were computed on the IBM 360/50 at the Australian National University. Double precision arithmetic was used for all except the computation of simple sample statistics. Some scatterplots were made on the PDP 10 at the James Cook University of North Queensland, in connection with analysis of the data presented in Chapter four.

Initially, simple sample statistics were computed on an Olivetti "Programma", a small calculator capable of being programmed to a limited extent. However, storage available on this machine is severely limited and the language of a very low level. Thus, its use was discontinued and all results computed on the IBM 360/50 using Fortran IV.

PROGRAM SOURCES

Programs used were obtained from a variety of sources and were written in a number of Fortran dialects. These were modified to run on the IBM 360/50 and changes to input and output were usually included. In some cases further facilities were written into the programs.

The program for computing simple sample statistics is a modified version of one provided by Sokal and Rohlf (1969) and that for computing the non-parametric simultaneous test procedure analyses was programmed from a method given by the same authors. Canonical variate analyses were computed using a combined version of two programs from Cooley and Lohnes (1962). Professor K.R. Gabriel of the Hebrew University, Jerusalem, provided the program for computing the simultaneous test procedure multivariate analyses of variance. The program for computing the canonical correlation analyses was from the IBM "Scientific Subroutine Package" although this was modified to permit computation in terms of standardised data. Multiple regression analyses were computed using a program written at the Division of Mathematical Statistics, C.S.I.R.O., Canberra, and modified for use on the IBM 360/50.

CHEMICAL ANALYSIS

During the course of the present study considerable chemical analytical work was carried out on litterfall

and litter material from the forest floor.

Elements assessed were nitrogen (total), phosphorus (total), potassium, calcium, magnesium, manganese, iron, zinc and ash.

Samples were ground in a "Wiley" mill to pass a 1.33mm. sieve. They were then dried at 105°C. overnight, cooled in a dessicator and weighed in preparation for analysis.

TOTAL NITROGEN AND PHOSPHORUS

These elements were determined using slight modifications of the methods of Williams and Twine (1967). Material for analysis was digested in a mixture composed of K_2SO_4 (200g.) and Se (1g.) dissolved in concentrated H_2SO_4 (1l.). Absorbance measurements were made simultaneously for both elements on a twin channel Technicon Auto-Analyser.

Phosphorus was measured as the development of "molybdenum blue" formed by ascorbic acid reduction of the phospho-molybdate complex formed from ammonium molybdate and sample phosphorus. Absorbance was measured at 660mμ.

Total nitrogen was determined by a modified Kjeldahl method using alkaline phenate and sodium hypochlorite. Absorbance was measured at 625mμ.

CATIONS

The remaining elements were determined by atomic-absorption spectrophotometry. Material for analysis was digested in a ternary acid mixture of H_2SO_4 (1 part), $HClO_4$ (7 parts) and HNO_3 (24 parts). Digestion was followed by filtration, appropriate dilution and absorbance measurement. For calcium and magnesium determination an excess of lanthanum was added during dilution to suppress possible interference effects.

PERCENTAGE ASH

Ash values were obtained by igniting approximately 0.5g. of ground sample material for three to four hours at 500°C.

COMPUTATION OF RESULTS FROM INSTRUMENT OUTPUT

Computation of individual results from the graphical or digital output of atomic-absorption spectrophotometers and autoanalysers can be very time consuming and subject to errors of various types.

These and a discussion of calibration models are presented in Spain (1970) (Appendix).

CHAPTER TWO

CONSPECTUS OF THE PROBLEM

INTRODUCTION

Aspects of plant nutrient element cycling in forest ecosystems have now been studied for nearly one hundred years. Most studies have concentrated on a restricted subset of component parts of the biological and geological cycles and, while the general nature of the principles governing mineral and organic matter flow is now known, it appears that little of the detailed work necessary to elucidate their precise forms has yet been performed.

The reasons for this are not difficult to discover and may be partly ascribed to the considerable labour requirements involved in collecting the required data. A further possible reason was, until recently, the lack of a suitable method for integrating the information obtained. This is now potentially available through the processes of systems analysis and simulation (Dale, 1970; Watt, 1966; Watt, 1968). Thirdly, many workers are influenced by their training and have tended to take an unduly restricted view of their subject. Other problems involve projects with inadequate statistical design often leading to collection of the wrong type of data, inadequate intensity in sampling, unwarranted extrapolation from measured values and ill advised choice of statistical

model for the relationships under study.

MATHEMATICAL MODELS

No ecologically realistic model of a natural ecosystem has yet been produced (Pomeroy, 1970) although approaches have been made in one grassland/savannah ecosystem (Bledsoe et al., 1971).

Several difficulties remain to be resolved before realistic models can be produced including the substantial problems of lack of knowledge of the real world and non-linearity of nutrient fluxes. Computational problems in the fields of both hard and software remain to be resolved and hybrid computers may be required for their solution (Pomeroy, 1970).

The study of microcosms has been advanced as a partial answer to the problems. The usefulness of this approach was demonstrated by Patton and Witkamp (1967) who used an analogue computer to solve a system of simultaneous rate equations describing the flux of 134 caesium flow through a microcosm. This microcosm consisted of air dried, radioactive leaves of Quercus alba L. and variable combinations of other compartments including microflora, millipedes, and soil. A forcing or driving function was introduced via the "litter" compartment.

Studies such as that described above and those of Neel and Olson (1962) are useful in elucidating the nature of specific relationships but suffer from problems of container effect and extrapolation to the real world.

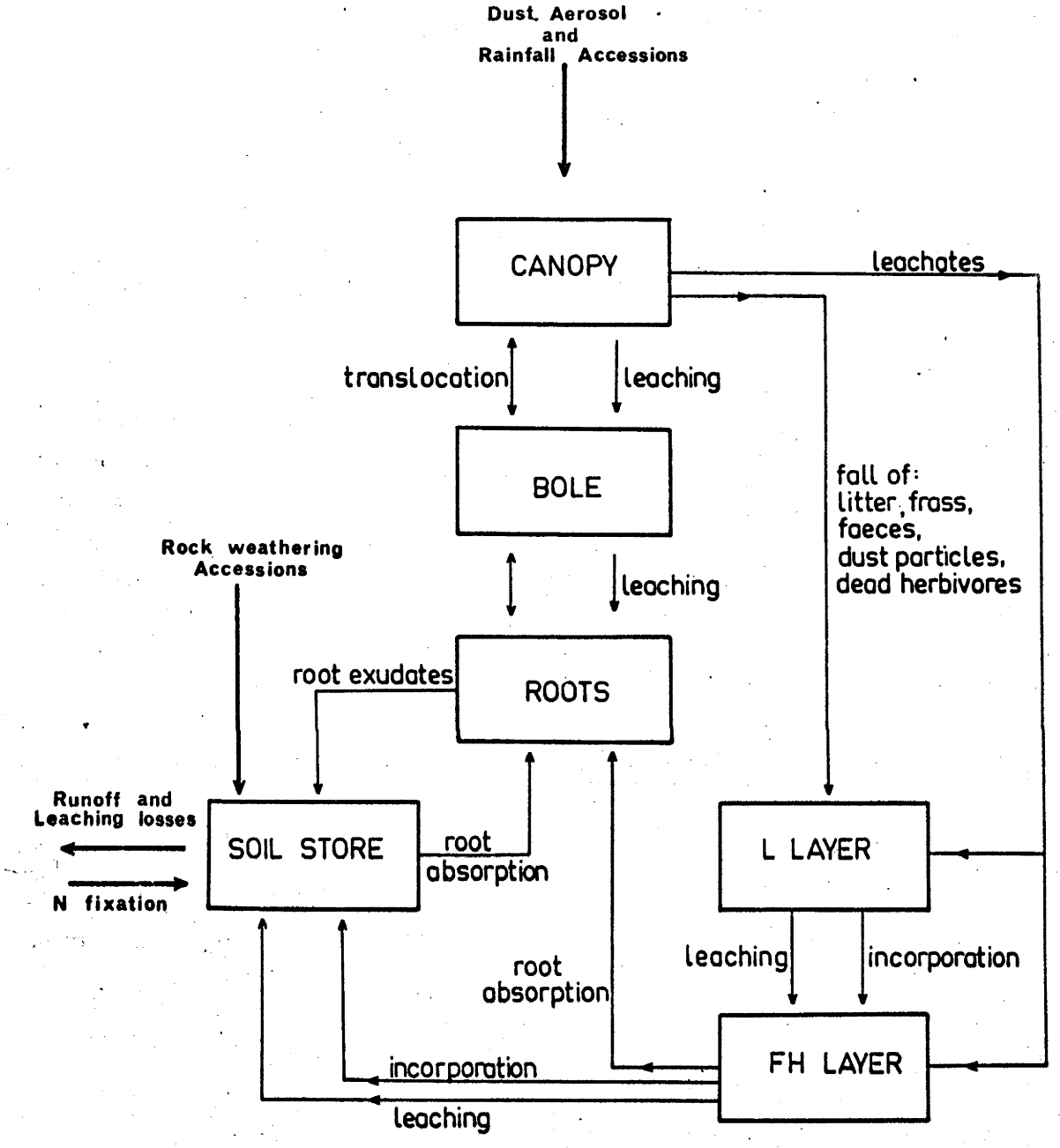

Fig. 1. Flow chart for forest ecosystem.

TABLE 2. Conceptual model for forest ecosystem - Elements and flows.

A. MAJOR ELEMENTS

(i) canopy)
(ii) bole) tree
(iii) roots)
(iv) L layer litter)
(v) FH layer litter) litter layers
(vi) soil store of available nutrients

B. MAJOR FLOWS

(A) INPUTS

(i) dissolved elements in rainfall
(ii) dust
(iii) rockweathering inputs
(iv) soil movements
(v) animal immigration
(vi) fertilizer input

(B) OUTPUTS

(i) leaching of elements to below root depth
(ii) volatilization losses
(iii) animal emmigration losses
(iv) removal of tree bole
(v) removal of cones
(vi) removal of litter

(C) INTERNAL TRANSFERS

(i)	litter fall	- leaves	to L
(ii)	litter fall	- bark	to L
(iii)	litter fall	- branches	to L
(iv)	litter fall	- female cones	to L
(v)	litter fall	- male cones	to L
(vi)	litter fall	- pollen	to L and FH
(vii)	litter fall	- dead boles	to L
(viii)	leachates	- canopy	to L
(ix)	leachates	- canopy	to FH
(x)	leachates	- canopy	to bole
(xi)	leachates	- bole	to L
(xii)	leachates	- bole	to FH
(xiii)	leachates	- bole	to soil
(xiv)	leachates	- L	to FH
(xv)	leachates	- L	to soil
(xvi)	leachates	- FH	to soil
(xvii)	leachates	- FH	to roots
(xviii)	incorporation	- L	to FH
(xix)	incorporation	- FH	to soil
(xx)	frass and other insect parts		to L
(xxi)	faeces		to L

It appears that it will be some time before ecologically realistic models of large ecosystems become available (Pomeroy, 1970). In the absence of any rigorous theoretical framework, progressive refinement of preliminary models by a process of interaction between the model and data collection from the real world may prove to be the most useful approach. It is further considered that, because of the interactions between plant nutrient elements, any realistic model of nutrient cycling must be multivariate in nature.

CONIFER FOREST NUTRIENT CYCLES

Cycling of elements within forest ecosystems has recently been reviewed in detail by Sukachev and Dylis (1964), Rodin and Bazilevich (1967), Ovington (1962, 1965, 1966) and also by several authors in Reichle (1970). Overall cycles are divided, perhaps arbitrarily, into biological and geological cycles.

Another concept is to regard the forest or a suitably delineated part of it, as an open, multivariate system with inputs, outputs, elements and interelemental flows of energy, organic matter, water, plant nutrient elements and other defined variables.

A tentative and generalized flow chart for the major mineral element flows in a simple, open forest ecosystem is given in Fig. 1. Elements, flows within the system and transfers into and out of the system, are listed in Table 1.

Although this is an extremely simple ecosystem and perhaps only approximated by forest plantations, the principles involved are capable of generalization to more complex "natural" forest ecosystems with multiple tiered canopies and well developed ground vegetation. However, their complexity poses considerable problems in parameter measurement.

The concept of an ecosystem followed here is that of Dale (1970) who defines it as an open system containing at least one living element.

ELEMENTS OF THE FOREST ECOSYSTEM

The primary entity of the forest ecosystem is the tree, more conveniently regarded as three distinct elements rather than a unit since flows occur to and from the canopy, bole and roots. The litter may also be regarded as a discrete entity but is best subdivided into two layers; the L and the combined F and H (FH) on the basis of the presence or absence of roots. The soil store of the plant nutrient element under study is one of the major elements of the ecosystem.

The various elements comprising the ecosystem are conceived of as reservoirs of the plant nutrient element under study. They can never be regarded as static since they are subject to net variation with ontogeny of the trees, the effects of natural disasters, flooding, erosion and many other variables.

Ovington (1962) presents weights of plant nutrient

chemicals in the various elements of forest ecosystems studied to that date.

Crown

Crown weight varies seasonally with a dynamic balance between production and the shedding of branches, flowers, fruits, cones and other material. The plant nutrient elements contained at any time in this crown may also vary independently following changes in the concentrations of those associated with leaf ontogeny and senescence (Kittredge, 1948; Miller, 1963b; Viro, 1955).

With ontogenetic development of the trees, total leaves, at least, attain their maximum weight per unit area quite early and this persists thereafter with little change or a slight decline (Ovington, 1965). In studies of Pinus radiata D. Don, Forrest and Ovington (1970) demonstrated this maximum level occurring at seven to nine years for branches and their leaves combined, whereas Pinus taeda L. foliage weights were at a maximum at 25 years while branchwood reached its maximum at approximately 45 years (Switzer et al., 1968).

Boles

The weight of boles increases in a sigmoid fashion after planting and may continue to increase throughout the life of the crop. Removal of boles during thinning operations

reduces this on an area basis (Ovington, 1965).

Roots

As stated by Ovington (1962), there appears to be little quantitative information on absolute root weights and turnover rates in forest stands. In comparison with proportions of above ground biomass Will (1966) obtained a figure of 0.69 times branch weight for roots greater than 1.3cm. diameter in an 18 year old stand of P. radiata but furnished no information on the ontogenetic changes which may occur. Ovington et al. (1967) presented data for an eight year old P. radiata stand indicating a figure of 0.63 for the same relationship. Ovington (1965) claims that roots usually exceed the combined weights of leaf and branch material but this is so for only certain of the species discussed by Ovington (1962).

The relationship is undoubtedly species specific and subject to considerable environmental modification. Accurate assessment of active root weights per living tree is difficult and especially so in thinned stands due to the phenomenon of root grafting which permits the survival of root systems after the bole of the tree is harvested (Graham and Bormann, 1966; Will, 1966). A further difficulty is the seasonality of growth (Ovington and Murray, 1968).

Even in mixed species stands transfer of plant nutrient elements may occur between taxonomically unrelated individuals (Graham and Bormann, 1966; Rovira,

1969; Woods, 1970). The ecological significance of this finding remains to be completely resolved as does the relative importance of the rôles played by, respectively, grafting and root exudates.

Litter

The forest floor may be regarded as one element of the system. However, constituent layers have the power to access material independently from different sources and roots are usually confined to the FH layer. Thus, it appears useful to regard them as two separate layers viz. the freshly fallen, largely undiscoloured material comprising the L layer and the remaining amorphous mycelial and humic material as comprising the FH layer.

In a natural, free seeding, closed canopy forest the opening of a space in the canopy through death of a mature tree allows seedlings formerly supressed by lack of light, and possibly root competition, to commence active growth. The dense mat of seedling trees will prevent much light penetration to the forest floor and permit little growth of ground vegetation allowing slight disturbance to the litter layers. Conifer planting is often preceeded by clear felling and burning producing an entirely different situation for the first few years at least. Seedlings are planted on an ash bed and, concurrent with their development over the first few years, they compete with a flourishing ground vegetation of ferns, grasses, shrubs and seedling trees of other species. Later in the

development of the crop, the ground vegetation is progressively suppressed and may virtually disappear after canopy closure or be restricted to scattered individuals of shade tolerant species, such as Pteridium esculentum (Forst. f.) (Forrest and Ovington, 1970). In some cases a virtual suppression at canopy closure may subsequently give way to a low level of understory growth (Ovington, 1959; Ovington, 1962).

It has been stated by many authors (see, inter alia, Forrest and Ovington, 1970; Minderman, 1968; Nye and Greenland, 1960; Olson, 1963; Reiners and Reiners, 1970) that after a number of years the weight of the forest floor reaches a steady state with gains and losses being approximately balanced. In climactic natural forests, subject to random replacement of trees, this steady state is probably in the nature of a true dynamic equilibrium since the saprobiota is most likely a mosaic of stages of development and recolonisation of any depleted area is rapid. Where large areas of conifers are planted on land formerly supporting broadleaf forest a new and uniform environment develops under the influence of the growing trees. This situation involves selection of a new saprobiota which probably develops through a number of seral stages. Colonisation from without is probably slow resulting in that subset of the original saprobiota capable of existing under the altered conditions. In this situation, an equilibrium in terms of weight may not imply a similar qualitative state. If a simple situation is considered in which litter fall inputs were static in terms of ratios

between leafy and woody material, a qualitative change would occur in the litter with time due to the differential susceptibilities of these litter fall components to decomposition (Alexander, 1965). Further, even a compound such as cellulose which may be present in both masked and unmasked forms (Handley, 1954) would undergo a weight increase over time and more resistant lignified material as in branches and female cones could be expected to increase to an even greater degree. Consequent upon this qualitative change in the litter must follow an increasingly rapid decomposition of the more readily assailable fractions. This, conceivably, could be due to an increasingly successful level of adaption of the micro and mesobiota of the litter layers occurring concurrently with the development of the trees. A problem with this model would be an ever increasing concentration of lignified material. Most likely, a restricted subset of the biota develops the capacity to break down certain fractions of lignified material but this equilibrium probably occurs, if ever, only at a later stage in the ontogeny of the trees. That the adaptation is not complete is suggested by the work of Tamm and Ostlund (1960) who report that soil organic matter under permanent forests contained certain fractions as old as 370 years as assessed by radiocarbon dating. Using the same technique Campbell, et al. (1967a, 1967b) obtained figures ranging from 25 to 1400 years. In spite of the probability that much of the organic matter in forest mineral soils is derived from above ground sources and may be more stable after incorporation, residence times of

resistant fractions are undoubtedly lengthy in the lower layers of mor litters.

The general problem of resistance to decomposition in lignins and other compounds is reviewed by Alexander (1965).

L Layer

As stated above, the L layer comprises mainly freshly fallen leaves and twigs. The leaves still retain their physical integrity and are little discoloured by fungal activity while the twigs appear to be virtually unaffected by decomposition processes. This apparently unchanged appearance does not imply that fungal activity has not occurred as saprophytic organisms, chiefly fungi, commence the cycle of breakdown well before leaf abcission (Hudson, 1968).

FH Layer

The FH layer, as here defined, comprises the F (fermentation) and H (humus) layers together with the small incorporation zone characteristic of conifer litter. These layers may, or may not, access material independently. If they do, they may need to be considered separately.

Soil Store of Ecosystem Requirements

The mineral soil has contained within it a quantity

of organic matter, plant nutrient chemicals, water and other compounds of importance to the forest ecosystem. The soil store of any requirement may be considered somewhat arbitrarily as the available portion of it lying within the root depth of the plant.

This soil store undergoes dynamic changes with the development of the tree as its roots grow to increasing depths. In the case of plant nutrient mineral elements, it may be equated with the available fraction. However, assessment of the available fraction of any plant nutrient element within the soil is a matter of some difficulty. Methods are available for assessment of the total amount of nutrient elements in any given soil. These usually involve the use of hydrofluoric acid to completely break down and solubilize all the mineral and organic matter present and take no cognizance of the particle size distributions and thus surface area of soil and the differing availability of elements contained in different chemical states. The determination of exchangeable nutrients also suffers from drawbacks in that rhizosphere acids may make mineral elements available from some depth within larger soil particles (Klausing, 1956 in Duvigneaud and Denaeyer-De Smet, 1970; Voigt, 1968).

Other factors impinging on the soil store of many elements include the increasing podzolisation, thus acidification, of the upper mineral layers with crop development and the concurrent leaching and redistribution of plant nutrient elements (Hamilton, 1965). The level of podzolisation is however species specific and

pH measurements indicate that certain species have more extreme effects than others (Ovington and Madgwick, 1957).

INTERNAL TRANSFERS

Materials move within ecosystems by a series of transfer processes. Rates of movement depend on the nature of the processes in operation which are, in turn, constrained by a number of extrinsic and intrinsic factors.

Extrinsic processes are those influences impinging on the system from without but not involving actual transfers of material and include the geological and climatological history of the area, the present climate, past vegetational history and certain of the cultural influences of man. They may be regarded as factors involved in setting such basal parameters of the ecosystem as soil fertility, soil depth, environmental temperature and water supply. Intrinsic processes circumscribe the ecosystem from within and comprise direct and indirect influences of the genotypes of the vegetational dominants. In forests, intrinsic factors control the eventual biomass of the system subject to extrinsic constraints.

Transfers within the system involve a complex of movements resulting in a net increase in the elements of the tree and the litter layers partly at the expense of the soil store of nutrient elements. Flow thus involves a net movement of materials in the direction soil $\longrightarrow$ plant biomass $\longrightarrow$ litter layers $\longrightarrow$ soil although considerable transfer occurs in the opposite direction.

Transfer Processes

These may be considered under the three categories of mechanisms involving transfer of material into the plants, mechanisms involved in redistribution within the plant and finally those involved in loss of material from plants and plant tissue.

Transfers Into The Plant

Mineral elements gain entry to plants through two major routes. Most important is the root absorption pathway and secondly the foliar route (Franke, 1967; Wittwer and Teubner, 1959).

Details of these processes are not considered here, only their net effects. In a given natural ecosystem they are intrinsic and thus not greatly subject to modification. This may not be true of artificial plantations where such cultural practices as thinning may permit an increased rate of growth in the remaining trees, possibly due to increased water and nutrient uptake consequent on a reduction in root competition.

Transfers Within The Plant

The dual processes of translocation and ion transport in the xylem and phloem streams are intrinsic to the system and their net effect may be assessed as the biomass change of any element over a given period of time.

Transfers From Plant Tissue

Material is lost from living and dead plant tissues by a number of pathways. These processes are considered below.

Litterfall

Litterfall from the aerial parts of plants has been studied by workers in a range of forest types and the principles governing its magnitude, seasonal and annual patterns are reviewed by Bray and Gorham (1964).

It is probably the most important vehicle for movement of material out of the plant and, through its varying proportions of leaf, woody material, male and female cones, qualitative as well as quantitative variation results. Qualitative variation also occurs through other mechanisms notably withdrawal of material from senescing leaves prior to abcission (Viro, 1955).

Root Turnover

Roots undergo a process of dissolution and replacement which may be of considerable magnitude when compared with litterfall (Orlov, 1955 and Remezov, 1959 in Ovington, 1962). However, the products of fine root dissolution are, presumably, in such a form that they may be readily reabsorbed.

Root Exudates

The nature and properties of root exudates have been reviewed by Rovira (1969) and it appears that the many compounds and elements involved may play a considerable role in interplant relationships. Exudates act through direct effects on the roots and seeds of competing species and indirectly through their effects on rhizosphere organisms and on nutrient release from soil minerals (Voigt, 1968).

Leaching

The term leaching as applied to the loss of material from plant tissue has been used to describe processes that are undoubtedly dissimilar. These are the dissolution and physical removal of material from litter and the removal of material from living foliage by the action of rain. For certain mineral elements such as calcium, manganese, phosphorus, potassium and sodium leaching from foliage accounts for considerable proportions of the total annual losses from the forest canopy (Attiwill, 1966; Madgwick and Ovington, 1959; Mina, 1966; Tamm, 1951; Will, 1959). A wide range of other substances are found in foliar leachates and these range in nature from simple carbohydrates to phytotoxins. The general principles governing leaching of material from plant parts are reviewed by Tukey (1970).

Leaching of mineral elements from litter is a different

process to that from intact and living tissue, and involves little more than dissolution and transport of elements made available primarily by fungal decomposition processes. Dissolution of organic matter is also dependent on its chemical nature and the presence of masking compounds (Handley, 1954). Thus, lignin is slow to breakdown due to its chemical nature while masked cellulose breaks down slowly because of the presence of tanning and other masking compounds.

The mycological successions occuring during the breakdown of leaves with their incorporation in the litter layers have been studied by Hering (1965) and Hogg and Hudson (1966) for broad leaved deciduous trees, Kendrick and Burges (1962) for Pinus sylvestris and Macauley and Thrower (1966) for Eucalyptus regnans F. Muell. In a review of this work Hudson (1968) considers that the usual process involves the infection of the leaves with weak parasitic and saprophagous fungi well before leaf fall. These fungi persist on the leaves for a considerable time after abcission before giving way to the more typical soil species. The fungi present on the leaves of any one species tend to be specific and thus during the early stages of breakdown at least, successions are probably unique. Rates of loss of elements vary with their nature. Sodium and potassium are generally lost very rapidly from decomposing tissue while other elements such as iron are scarcely lost or not at all. Location within the cell is also important with some elements and in the case of calcium in Casuarina litter, loss proceeds in two phases.

The first coincident with dissolution of the cell contents and the second with breakdown of the cell wall (Burges, 1956). Mobilities of the major nutrient elements are reviewed by Rodin and Bazilevich (1967).

Incorporation

Loss of material from litter may involve its incorporation into the mineral soil through the action of soil animals. Earthworms are efficient in mull litter but few are present in mor, a niche not very efficiently filled by arthropods.

With the possible exception of earthworms, the rôle of soil animals in decomposition and incorporation is not yet well defined but current concepts are reviewed by Edwards et al. (1970) and Kevan (1965).

Minor Losses

Plant material and its contained elements are lost from the canopy through pollen, flower and seed production (Ovington, 1963). Part of the first, at least, may be entirely lost to the ecosystem through wind effects.

Further losses from the canopy and roots may be caused by herbivore browsing. Both roots and foliage are affected and, in the case of an epizootic, may be extreme to the point of completely defoliating the canopy. Mineral content of birds and selected insects

in the above ground portion of a Pinus sylvestris ecosystem were presented by Grimshaw et al. (1958). These authors concluded that, although the actual biomass of these animals is small compared with that of the foliage, loss of plant material may be significant when amounts passing in frass and faeces are considered.

Emigration of animals from an ecosystem may occasion a loss although this is probably balanced by immigration over a long time period.

EXTERNAL INPUTS AND OUTPUTS

These transfers without the defined open system are also known respectively as exogenous and endogenous flows (Dale, 1970) and may be arbitrarily divided into two groups; the natural and those due to the influence of man.

Inputs

Natural Inputs

Natural inputs to the forest ecosystem may be divided into those resulting from biological activity and those originating from geological or atmospheric sources.

Geological inputs are principally derived from physical weathering of rock particles releasing elements to the soil solution and rhizosphere and thus

to the plants. Soil erosion and flooding may achieve a similar site enrichment where the ecosystem is low in a catchment. Volcanism may enrich an ecosystem or destroy the living elements through the deposition of lava (see, for example, Dyer and Hicks, 1968). In both cases, the extent of enrichment will depend on the chemical nature of the ash; base rich basaltic showers usually give rise to a fertile soil whereas others, rhyolitic or andesitic in nature, may not.

Dust and elements dissolved in rainfall provide a constant addition of elements to forest and other ecosystems. The canopy acts as a trap for dust and aerosol particles which may later be washed through the canopy by rain (Ovington, 1962; White and Turner, 1970). Inputs of dissolved elements in rain have been studied by, inter alia, Allen et al. (1968), Attiwill (1966), Erikson (1952), Hutton (1958, 1968), Hutton and Leslie (1958), Madgwick and Ovington (1959), Nihlgardh (1970), Wetselaar and Hutton (1963) in recent years. Earlier studies are reviewed by Kittredge (1948).

Hutton (1968) considers that, away from the coast, a large proportion of elements accessed in rainfall are derived from terrestrial rather than marine sources and thus represent a cycling, or possibly a transfer of elements from one ecosystem to another rather than a marine derived input.

Studies of rainfall accession of elements to forest ecosystems have been conducted by, inter alia, Attiwill (1966), Madgwick and Ovington (1959), Miller (1963),

Tamm (1951) and Will (1955, 1959) which demonstrate that considerable amounts of plant nutrient elements are deposited over the course of development of forest crops. Ovington (1962, 1965) calculates that rainfall derived inputs may approximate losses of certain elements due to harvest removal of boles.

Nitrogen accession is one of the more critical inputs to forest and other ecosystems since it may frequently limit plant growth (Ovington, 1962; Mishustin and Shilnikova, 1969; Mulder et al., 1969) or decomposition of organic material with a high carbon to nitrogen ratio (Freidel and Attiwill, 1968).

Fixation of atmospheric nitrogen is probably the most important source of supply and may be made available to the plant element of the system through the medium of root nodules on members of the Leguminoseae or on genera as taxonomically diverse as Alnus, Casuarina, Ceanothus, Discaria (Bond, 1967). This has been utilized in commercial forestry practice and the work of Gadgil (1971) in demonstrating the beneficial effect of lupin as a shelter crop on nitrogen supply to Pinus radiata growing on sand. The soil microflora is the second important source of atmospheric nitrogen fixation with bacteria and algae as the most active causal agents. A further undefined source of nitrogen fixation has been recorded by Stevenson (1959).

Inputs Influenced By Man

Man affects inputs to ecosystems both directly and indirectly. Direct effects include such obvious inputs as organic or inorganic fertilizers. Indirect inputs occur as a result of other activities of man.

Direct Inputs

In forest ecosystems, growth rates of most living elements are affected by the application of chemicals whether they be applied to promote growth of the tree crop or reduce some element of the biota.

Benefits in the form of increased uptake of elements by the tree crop and subsequent increases in growth rates have been documented by various authors following application of fertilizers to forest soils, although luxury consumption of plant nutrients apparently unaccompanied by increased growth rates has also been recorded. (Weston, 1958; White and Leaf, 1956). A recent symposium (Tennessee Valley Authority, 1968) reviews current concepts of forest fertilization. Some of the negative results of pesticide and fertilizer usage considered by Tanton (1970) include supression of nitrogen fixation, induction of unavailability of certain trace elements and the promotion of eutrophication in waterways. Fertilizers may also have profound effects on the litter layers (Viro, 1963).

Biocidal chemicals of various types have been applied to forest ecosystems to control defoliating insects (Morris,

1963; Newman, 1964), pest mammals (pers. obs.; Rudd, 1966), suppress fungal diseases and to reduce competition in the seedling stages of growth where plantations are being established. Environmental effects of these chemicals are reviewed by Cope (1971), Moore (1967), Newsom (1967) and Rudd (1966). In the case of pesticide application a major result will probably be considerable disruption of the natural balance of decomposer populations (Alexander, 1965 and 1969). This is especially true of pesticides lodged in the litter layers of mor forming species since the high organic matter levels slow their degradation (Edwards, 1966). They also cause reduced uptake of a number of chemical elements (Martin, 1963; Wilde, 1958).

Indirect Inputs

Air pollution from industrial sources may be a particularly important influence. Phytotoxic effects on both broad leaf and conifer species resulting from exposure to such pollutants as ethylene, fluorides, ozone, peroxyacetyl nitrates and sulphur dioxide are reviewed by Brandt and Heck (1968), Dugger and Ting (1970) and Thomas (1951). More subtle effects are prevalent including a general darkening of the landscape close to industrial areas, death of arboreal lichens and the selection in certain Lepidoptera of melanic genotypes over their lighter coloured typical forms (Kettlewell, 1961). Radioactive pollutants may be especially important given the relatively high levels of sensitivity of trees to ionizing radiation

(McGinnis, 1963; Woodwell and Marples, 1968; Woodwell and Rebuck, 1967). They are known to be present in trees and pulpwood as a result of nuclear testing in the atmosphere (Fraser and Gaertner, 1970).

Outputs

Materials lost from the ecosystem often move by essentially the same processes that cause acession. Both may occur at any one time and only a net effect of loss or gain to the ecosystem recorded.

Outputs may also be divided into those naturally operative and those induced by the presence of man.

Natural Outputs

Rainfall, through its ability to leach a range of substances from foliage, stems, bark, litter and soil acts as a vehicle for loss of these materials when they are carried in runoff water or leached to below the level at which they can be absorbed by plant roots.

The fact that any measurements taken represent a net affect of inputs and outputs makes the contribution of the weathering of soil particles to the plant nutrient element status of the ecosystem difficult to measure. Studies in certain "water-tight" ecosystems represent one approach (Bormann and Likens, 1969). These investigators selected a catchment with an impermeable bedrock and, by measuring inputs of elements derived from rainfall and

outputs through a weir located on the stream at the exit to the catchment, estimated by difference the amounts lost from the system due to soil and rock weathering. The drawback with this "black box" approach lies in the assumptions made. Bormann and Likens (loc. cit.) assumed that because the vegetation of the catchment was climactic no net change in biomass took place over the course of their measurements. However, ecosystems are dynamic in nature and thus have an implicit temporal component in their definition. Therefore, any likely biomass change in the ecosytem would tend to reduce the value of their results (Lutz, 1963; Major, 1970; Ovington, 1962; Pomeroy, 1970). The necessity to make such untestable assumptions weakens this so-called "black box" approach.

Erosion and run off losses may result from baring of the soil due to grazing or burning the forest floor. Forests normally do not suffer much loss in this way due to the stabilizing influence of litter layers and tree roots. In particular, any factor disturbing the litter layers will tend to promote losses through this medium and in New Zealand, introduced ungulates (notably Capridae and Cervidae) have induced considerable losses of litter and topsoil in many forests in the drier areas.

Burning may be a direct source of loss of certain elements such as nitrogen, carbon, sulphur and phosphorous. The latter starts to be lost at temperatures greater than 400°C. (Dormaar and Webster, 1964) which are not uncommon in forest fires (Ahlgren and Ahlgren, 1960). Also, losses of a range of elements in smoke during heath burning.

have been demonstrated to be of considerable magnitude (Allen, 1964; Lloyd, 1971) and this is unlikely to be different in the case of forest fires. Further, by solubilization of mineral elements, it increases the likelihood of runoff and leaching losses. The general effects of burning on forests and their soils are reviewed by Ahlgren and Ahlgren (1960), Burns (1952) and Viro (1969). It is considered by the first of these authors that, because of the many contradictory results of work on forest fires few generalizations are possible. Apparently, this topic would repay more rigorous investigation.

Other natural losses include those of wind borne plant parts which may be blown out of the ecosystem, emigration of animals and dentrification. Losses from the first two agents are probably small and will be at least partially balanced by inputs of the same type where the ecosystem under consideration constitutes part of a larger area of a similar nature. As stated above, losses of nitrogen are more serious in terms of optimal production.

Outputs Influenced By Man

Man influences outputs from the forest ecosystem through a variety of channels. Activities in harvesting boles and other plant parts, game and his cultural processes all involve possible loss of nutrient capital either directly or indirectly.

Harvesting Losses

Harvesting the tree crop usually occurs in a number of phases in artificial plantations. Initially, the stand is thinned at the stage when posts are available to be followed some few years later by removal of poles. Clear felling occurs near maturity and the timing of this is dependent on the final products required. For example, trees grown for pulpwood production are harvested earlier than those destined to be milled as saw logs. Ovington (1962, 1965) in discussing harvest losses makes the point that although instantaneous losses at the time of clear felling appear large, when these are considered on an annual basis levels are considerably lower than those for agricultural crops. Removal of the bark and green crown may cause a much more serious loss of nutrients and, for this reason, Christmas tree production may be considered deleterious.

Other products such as seed and litter are harvested from forests. Litter harvesting, if conducted on a large scale, may seriously deplete a site especially if the underlying soil is not rich in nutrient elements (Kittredge, 1948). The subject of litter harvesting occasioned much controversy in Europe in the latter part of the last century where considerable amounts were removed for stabling and mulching purposes. This early literature is reviewed by Alway and Zon (1930) and the nutrients contained in the litter costed as fertilizer "equivalents". Although this approach may appear somewhat simplistic in the light of

today's knowledge, it did demonstrate the importance of litter in maintaining production in forests. In Australia, litter is still harvested for use in forest nurseries but the magnitude of removal is small and not regularly repeated in the same place thus reducing the likelihood of any serious effect.

Game is harvested from many forest ecosystems and, in Australasia, may comprise ungulates, macropods or birds. In terms of nutrient capital removed, losses are probably small but in the multiple use of the ecosystem considerable recreational value is gained as long as hunting pressures are not such as to endanger indigenous species. In New Zealand a different situation exists with introduced ungulates, principally Cervidae, endangering the stability of indigenous forest ecosystems especially in the drier areas. This results from the introduction of browsing mammals into an environment that previously supported in this niche only a few large birds, now extinct. The present policy of eradication cannot be achieved, and aims are moving towards accepting the presence of these animals and relying on a high level of predation by hunting pressure for control.

Cultural Activities

Through his cultural activities man exerts a considerable force on the balance of forest ecosystems. These may be considered under the headings of fire, grazing and silvicultural activities.

Fire has a profound effect on the forest ecosystem and affects all the elements from the tree crop to the biota of the forest floor. It may destroy the whole crop of trees or, depending on the meteorological conditions and fuels available, may only destroy the litter layers and ground vegetation. In fact, prophylactic or prescribed burning is commonly employed in the indigenous forests of Australia to reduce fuels in the cooler times of the year thereby avoiding large scale hot fires during the late summer period. An inevitable result of this is a considerable loss of nitrogen and other elements in smoke. Also, repeated burning of an area will tend to select the more fire resistant species. During preparation of indigenous forest sites for planting with conifers, a common practice is for the best of the original trees to be removed for saw logs and the rest pushed over with heavy machinery and burned. This must also involve loss of substantial quantities of nutrient elements.

Grazing is another factor in multiple use of forest ecosystems and its effects do not appear to be fully resolved. In some forests damage to the litter layers and compaction of the surface roots has resulted in reduced rates of tree growth, baring of the soil and subsequently erosion. In more open forests effects are probably less severe.

Silvicultural Activities

The various preparatory techniques such as burning

and soil baring with machinery potentially involve direct losses through volatilization and solubilization as well as indirect losses through promotion of erosion. Forests generally stabilize well the soil by covering it with a blanket of vegetation while the deep rooting trees hold it together to a considerable depth. However, in the interval between commencement of preparatory silvicultural techniques and crown closure considerable runoff and other erosion losses may occur. Later in the ontogeny of the crop, further risks of induced erosion losses are potentially present due to harvesting procedures.

CONCLUSIONS

From the information discussed above, the forest ecosystem may be seen as an open multivariate, dynamic, interactive entity. Its enormous complexity may be inferred from that of the many inputs and internal transfers. In many cases (e.g. root exudation) too little appears to be known of their magnitude and exact natures to be able to assess their practical importance. Interactions between chemical elements appear not to have been studied in any detail.

At the moment, there appears to be too little known about the forest ecosystem to be able to build rigorous simulation models, a statement that can perhaps be extended to biological systems in general (Pomeroy, 1970). This should not prevent the construction of preliminary models and the subsequent required interaction between the model

and experimental data collection from the "real world". This approach is probably the most profitable to pursue since it allows progressive refinement of the model. It also provides a guide to collection of the relevant information and ensures that it is of an appropriate form.

The most useful feature of the systems concept is the holistic overview provided. In the synthetic view of the forest system, biological and geological cycles merge since the effect of mineral elements on the system is generally independent of their origin. This does not imply negation of the useful analytic and pedagogic concepts of the two separate cycles but the latter may perhaps prevent their resynthesis into a viable conceptual whole.

It would appear that Pomeroy (1970) is probably correct in his claim that ecologically realistic models are some years distant although preliminary models will undoubtedly appear with greater frequency in the near future.

CHAPTER THREE

LITTER FALL: A MULTIVARIATE COMPARISON OF PLANT NUTRIENT ELEMENT STATUS AND RETURN IN FOUR SPECIES

Both the magnitude and chemical composition of litter fall from trees affect the development of forest soils and, ultimately, forest systems. Litter fall is a potent soil forming influence acting as a major transfer mechanism in the circulation of mineral elements and containing a wide range of complex organic compounds varying in biological degradability. The influence of a particular tree species on any given forest soil is largely a function of the ratios and absolute levels of these chemicals.

To gain further information on the litter fall component in the system, and as part of a larger study of mineral nutrient cycling, the litter fall of four species of exotic Coniferae Pinus lambertiana Douglas, Pinus nigra Arnold var. maritima (Aiton), Pinus ponderosa Douglas and Pseudotsuga menziesii (Mirbel) was compared in terms of magnitude, chemical composition and seasonal distribution.

Field work for the study extended from 13 November, 1968 to 12 May, 1970.

Plate 7: Temporary litter trap. Cpt. 53, Bago State Forest.

Plate 8: Permanent litter trap. Cpt. 53, Bago State Forest. Rain gauge 12.7 cm. diameter.

METHODS

LITTER FALL COLLECTION

Collections of litter fall were made from randomly placed traps at irregular time intervals throughout a period of approximately eighteen months (Table 3). All plots were sampled at each date shown.

Two types of apparatus were used to sample litter fall. Collections one to three were made using sieves with fine wire mesh bottoms. These were either round (47.6cm. in diameter with 9.5cm. walls) or square (sides 71.7cm. with 10cm. walls) (Plate 7).

The design of the litter fall traps used for collections four to seven was based on that of Ovington and Murray (1964) (Plate 8).

Forty of these traps were set out at random in each of the four study plots. All traps had a catching area of 0.266sq.m. giving a total sampling area of 10.64sq.m. in each plot.

SAMPLE COLLECTION AND TREATMENT

On each sampling occasion litter fall traps were emptied into large photographic trays and the contents transferred to paper bags. The samples were returned to the laboratory and dried for five days in a forced draught oven held at 80°C.

After drying, litter fall from each sampling unit

was sorted and weighed as leaves, woody material, male cones and female cones. All fractions were recombined and the total material from each sampling unit ground to pass a 1.3mm. sieve. This fine material was then mixed thoroughly and retained for determination of its ash content and concentrations of nitrogen (total), phosphorus (total), potassium, calcium, magnesium, manganese, iron and zinc. Sodium levels were determined for sample seven only.

DATA ANALYSIS

Data Sets

The data were treated in two ways. Firstly, matrices of sample elemental concentrations in the total litter fall were analysed and then, separately, sample matrices of the rate of fall of the individual elements assessed. The data set used for the latter analysis was generated by multiplying each matrix of sample elemental concentrations by the corresponding vector of total litter fall weights. To allow sample comparisons, the matrix products thus produced were divided by their associated sample intervals to provide the final rate of fall data matrices.

A combination of CVA and Gabriel's (1968) STP were used in the present study to analyse the chemical nutrient status of the litterfall samples described above. All concentration data were analysed as angles (inverse sine transformation) and the rate of fall data as their natural logarithms.

Difficulty was encountered in achieving even approximate homoscedasticity in sample ash values. Thus, to meet the assumptions of the multivariate methods, data for this variable were deleted and analysed separately using Sokal and Rohlf's (1969) modification of the non-parametric STP of Dwass (1960).

RESULTS

In describing results, a coding system is used to identify samples. This system is based on the specific name of the species under consideration and the sequential number of the sample. Thus, the fourth sample from the P. lambertiana plot is designated L4.

DATA SUMMARIES

Mean weights and 95 per cent. confidence limits are presented in Table 4 for all physical litter fall fractions for all samples. Asterisks in the table denote that confidence limits for the parametric mean include zero. Table 5 presents estimates of the weights of all physical fractions input to the litter system over the 365 day period from 7 May, 1969. Estimates of weight for the part of sampling interval seven involved were calculated from values for the whole interval. Assessed mean concentrations of the eight plant nutrient elements and ash values measured are presented in Table 6 for samples four to seven. The data are expressed in parts per million of

oven dry weight except for the sample ash values which are presented as percentages. Estimates of the weights of various chemical elements input into the litter layers over each sample period, and also for the 365 day period from 7 May 1969, are presented in Table 7. Again, the total figures are based on those for samples four to six and the appropriate fractions of the values for sample seven.

STATISTICAL ANALYSIS

Ash Analysis

The results of the non-parametric STP analyses computed for both data sets are presented in Table 8. In this table, non-significant subsets are erected at the $P<0.05$ level.

Analysis of Remaining Elements

Canonical Variate Analysis

CVA was carried out on both the concentration and rate of fall data for each species, both separately and combined. For all analyses significant eigenvalues ($P<0.05$) and the percentages of total variance explained by each are presented in Table 9. Their associated eigenvectors are presented in Table 10 as normalised discriminant function coefficients. Table 11 presents the eigenvectors scaled by multiplying each by the square root of the

corresponding diagonal elements of the "within" matrix to show the contributions of each variable to the computed functions.

Plots of mean canonical points for all analyses are presented for the concentration data in Figs. 1 to 5 and for the rate of fall data in Figs. 6 to 10.

Simultaneous Test Procedure Analysis

Both data sets were analysed for all combinations of variables and samples using the maximum characteristic root STP at $P<0.05$. Each species was analysed over samples four to seven and the four species were also compared within each sample interval.

For each analysis a total of $(2^4-4-1)(2^8-1) = 2805$ null hypotheses were tested. This being the number available for consideration when all combinations of the eight variables and four samples are to be analysed.

The results of these analyses can be summarised in tables of maximal acceptable or minimal rejected null hypotheses at any desired significance level. The implication relationships of these are discussed in detail by Gabriel (1968) where the method and its statistical justification are presented.

The results of all STP analyses conducted are presented in Tables 12 to 15 as lists of maximal acceptable null hypotheses at the $P<0.05$ level.

INTERPRETATION OF RESULTS

ASH ANALYSIS

The analyses of the sample ash values (Table 8) are considered both with regard to the concentration and to the rate of fall of the ash elements.

Results of the concentration analysis suggest that the three Pinus species form a group distinct from Ps. menziesii in that they show a common seasonal pattern of variation. However, mean levels and amplitudes of variation differ between each of these species. Ps. menziesii, exhibited little seasonal variation in concentration with only the extreme samples differing at the $P<0.05$ level. Peak levels within the Pinus group tend to coincide with the period of least litter fall.

The large weight of litter falling at sample interval seven has obscured the pattern of values that emerged from the concentration data. Litter fall rates were highest for all species over this interval and no species associations could be detected in plant nutrient element rate of fall data. The increasing order of the species in their annual contribution of ash elements to the forest floor is P. ponderosa, P. lambertiana, P. nigra var. maritima, Ps. menziesii, as calculated from Table 7.

MULTIVARIATE ANALYSIS OF REMAINING VARIABLES

Pinus lambertiana

The data for this species reduced to two useful dimensions for both the concentration and rate of fall analyses (Table 9).

Total nutrient status in the litter fall of this species reached its maximum between late October and late January. The levels dropped sharply in the following period from February to May when nutrients are withdrawn in considerable quantity during senescence prior to the period of major leaf fall. All samples differed significantly considering every element simultaneously (Table 14).

The analysis of the rate of fall of all elements taken simultaneously reveals a different pattern from that of the concentration analysis. The period of major litter fall, late January to May, was also the period of the greatest addition of plant nutrient elements to the forest floor and conversely the period with the highest litter fall nutrient status corresponds with that of least addition of plant nutrient elements to the litter layers. All sample periods were significantly different from one another considering all elements simultaneously although certain elements did not vary significantly over some sample intervals (Table 14).

Pseudotsuga menziesii

In both the concentration and rate analyses only two useful dimensions were retained. Sample interval five had the highest nutrient element status and interval four the lowest.

The pattern emerging from analysis of the rate of nutrient addition is somewhat different. Sample intervals five and six, although highest in nutrient status, are lowest in terms of their addition of plant nutrient elements. These two samples are not significantly different considering all elements simultaneously (Fig. 7, Table 14). However, all other elements in the analysis varied significantly between all other samples and between samples five and six combined.

Pinus nigra var. maritima

Three useful dimensions were retained for both concentration and rate of fall analyses of the data from this species. All groups proved different on all elements simultaneously. The order of increasing plant nutrient concentration on axis I was samples 4,7,5,6, with samples four, five and seven forming a distinct group of lower plant nutrient status than sample six. The rate of fall analysis produced a different pattern with samples four, five and six having similar loadings on axis I and sample seven somewhat higher. On axis II there was considerably greater spread than for the concentration analysis.

Pinus ponderosa

The concentration analysis reduced to three useful dimensions (Fig. 4). All samples were significantly

different from one another and no obvious groupings tended to emerge. Sample six had high loadings on axes I and II, a factor that may be partly ascribed to the high iron concentration at the time of this sample (Table 6). The STP analysis of the concentration data revealed a somewhat complex pattern of maximal acceptable, non-significant null hypotheses with calcium exhibiting no significant variation over all samples. All samples differed from each other when all elements were considered simultaneously.

The rate of fall analysis, as expressed on the two useful axes I and II, presented a different pattern with samples four, five and six possessing similar loadings on axis I and the expected high loading on sample seven causing it to be somewhat separate. All samples were significantly different from each other (Table 14).

COMBINED ANALYSIS

A canonical variate analysis of both the rate and concentration data was computed treating each data set as a problem of 16 groups. Although this is not a rigorous approach, it may be used to indicate probable interspecific relationships and suggest common seasonal tendencies among the species.

For the concentration analysis three roots were considered which together exhibited 73.9 per cent. of the total variability. All species were separate with Ps. menziesii tending to be distinct from the Pinus group. Within the latter group the species remained

separate over samples four, five and seven but during sample six there was a distinct tendency to grouping with samples L6, N6 and P6 being closer to each other than to the remaining samples of their respective species.

The corresponding rate of fall analysis was examined on three roots exhibiting 83.0 per cent. of the total variability and revealed a rather different pattern. No clear separation between the species emerged and the four samples L6, M5, M6 and N4 were not separated to any degree. However, a seasonal trend showed with the four samples L7, M7, N7, and P7 having high scores on axis I while the remaining samples formed an elongate group without obvious species structure. No further meaningful structure could be discerned on axes II or III.

The holistic appreciation afforded by this form of analysis indicates that, although the litter fall of each species has its own distinctive seasonal cycle of plant nutrient variation, there is little difference between their seasonal patterns of nutrient addition to the forest floor. However, the total annual amount of elements supplied did show some variation between species both in absolute values and also in the amplitude of their individual nutrient status.

DISCUSSION

SAMPLING

On the basis of the preliminary variance estimates

obtained from sample one, a size of forty sampling units was chosen as appropriate for assessment of total litter fall weights. Sample size estimates of this nature can only serve as approximate guides due to the seasonal and annual variation exhibited by litter fall. This also applies to the sampling of many other biological phenomena. A problem in the design of experiments of this type includes that of obtaining satisfactory sample estimates for woody material and reproductive structures. Sample frequency distributions of both these fractions are often markedly skewed to the right and large weights, as from a broken branch, in one or two sampling units may have a disproportionate influence on the distribution of sample values. This may influence the frequency distribution of total litter fall values over any one collecting period. Female cones also pose a sampling problem in that their fall is erratic between years and rare within any sampling period. Thus, a very large sample size is required to allow the assignation of confidence limits for the parametric mean that do not include zero. This is illustrated in Table 3 where the confidence limits for this fraction frequently include zero. Also, since they tend to fall as discrete units the sample distribution in terms of weight may usually be expected to show a degree of right skewness. In the present study this latter effect was ameliorated by animal damage. White cockatoos (Cacatua galerita) cause damage to female cones in situ on the trees and considerable quantities of damaged and partial cones were recorded in the litter traps, tending to obscure the normal pattern

of female cone fall.

A further problem to be considered in the design of sampling plans for assessing litter fall is the size of the collecting device. This must be fixed according to the aims of the experiment and two main factors are of importance here. The first is the size of the material to be sampled. The opening of the collecting device must be considerably larger than the largest unit of litter fall to be collected. For example, the size of traps designed to sample needle fall of Ps. menziesii could be much smaller than those required to sample the foliar fall of broad leaved species. Branch and trunk litter are extreme examples of this and the peculiar problems associated with sampling these elements accurately are not considered here. The size of the collecting device depends also on the weight of material to be collected over each sampling period. This again depends on the aims of the experiment and if, for example, material was required for chemical, calorific and biochemical analyses the size of each collecting device would have to be large enough to ensure that adequate material was collected at each sample interval to meet the needs of all. This requires that yearly minima for each sampled fraction be known, or estimable on the basis of other work. A related factor here is the frequency of sampling and this must also be considered when calculating minimum amounts required for analysis. Obviously, all aims and requirements must be carefully considered a priori in light of the above factors to achieve an efficient sampling plan.

Sampling in the latter part of the present study proved adequate to meet all requirements although larger twigs and small branch fragments were probably under-sampled due to the limited size of the collecting devices used.

The litter traps used for samples four to seven proved satisfactory. The tubular polythene material was durable enough to withstand weathering and the considerable weights of snow that gathered in them periodically during two winters of the study. The traps also proved easy to empty and reset requiring approximately eight man-hours labour to service the 160 units in the present study. Animal influences on the traps proved slight. Certain pentachlorphenol treated posts were chewed by rabbits and one polythene tube was damaged by parrots.

The temporary traps used in the first part of the work were considered unsatisfactory, since they were subject to loss of material through wind swirling. They may also be interfered with by animals, a process that is not always recognised as having occurred. In the present study occasional rabbit faecal pellets were noted.

LEACHING LOSSES

The concentration values for the more mobile elements, and all other data dependent on them, must be considered minimal since no correction was made for leaching losses over the sampling periods. It is considered that correction factors such as those propsed by Kirita and Hozumi (1969) should not be applied unless the local values

of the parameters are known and are estimated at the same time as the litter fall measurements are made.

STATISTICAL METHODS

The statistical methods used proved appropriate to the problem and satisfactory resolution of sample differences was obtained.

CVA was, in all intraspecific comparisons, effective in reducing the magnitude of the sample space to a more easily interpretable two or three useful dimensions. The results of the CVA were complemented by the STP analyses and provided the exact significance tests required. This latter form of analysis also resulted in a very economical expression of sample differences through its implication relationships. One possible drawback of the method is its relative expense in terms of computation time when all combinations of samples and variables are being considered. The relevance of this factor increases sharply as more variables and/or samples are added to the analysis.

The non-parametric STP used for the location analysis of the ash values is a useful method when the data is such that a parametric analysis is not applicable and where the constraint of equal sample sizes is met.

COMPARISON WITH OTHER STUDIES

Of the four species studied in the present work one, Pinus lambertiana, appears not to have been studied before,

thus no comment can be made on its intraspecific variation. This is not the case with the other species and certain limited conclusions may be drawn on comparison of their nutrient status with other published records.

In general, detailed comparisons with other published work were not considered advisable due to the discrepancies in methods of chemical analysis.

Magnitude of Litter Fall

The physical weight of the recorded litter fall does not appear to depart greatly from values obtained in other countries for the same species. For Ps. menziesii values are slightly higher than those recorded by Will (1959) for New Zealand and Dimock (1958) for the Northern USA. Values recorded for P. nigra in the present study are intermediate between those of Will (1959) and those of Bomerle (1906, in Bray and Gorham, 1964) for Austria. P. ponderosa values are larger than those recorded for leaf fall by Biswell and Schultz (in Bray, 1964) and total fall by Jenny, et al. (1949).

It is of interest to compare values obtained in the present study with those obtained for Pinus radiata D. Don since this is undoubtedly the most widely grown plantation species in Australasia. All species in the present study returned less weight of litter to the soil than the New Zealand P. radiata plantations described by Will (1959). Both the three Pinus species and Ps. menziesii were within the lower part of the range of the weights measured for

P. radiata by Hamilton (1964) in the Australian Capital Territory. However, all Pinus species returned greater weights to the forest floor than those recorded by Pawsey (1959) for P. radiata in South Australia. The values for the Pinus species obtained during the present study were larger than those of Forrest and Ovington (1970) for P. radiata grown in the Southern Tablelands region of New South Wales where the present study was conducted. However, the trees in the latter study were considerably younger.

As compared with the indigenous vegetation the weight of total litter fall fell within the range of values given for Eucalyptus species by Bray and Gorham (1964).

Concentrations of Elements in Litter Fall

The concentrations of most elements lay within the ranges quoted for North America, Europe and Asia by reviewing authors Rodin and Bazilevich (1967).

It is of interest to compare the values obtained in the present study with those of Will (1959) for the species common to both studies, Ps. menziesii and P. nigra. In the present study nitrogen and phosphorus were greater, calcium was approximately the same and magnesium and potassium were slightly less than the values in Will (loc. cit.). English values (Wright, 1956) for P. nigra growing on sand were generally greater than those obtained in the present study except for calcium which was approximately equivalent and nitrogen which was less.

Weights of Elements Returned in Litter Fall

Within a species, the weights and ratios of the elements returned to the forest floor in litter fall tend to vary with site quality, altitude and latitude. However, some comparisons may be usefully made between locations where these independent variables do not vary too markedly.

In the Australian region the only study of litter fall in conifers available for comparison with the present is that of Will.

The weight of the annual nitrogen input to the litter layers was much greater in the present study than for all species considered by Will. Levels for P. ponderosa were more than double those for P. radiata and at least three times those of Ps. menziesii. Phosphorus levels generally tended to be somewhat lower in the present study, while potassium return was approximately equivalent. In the case of calcium the weights for P. lambertiana, Ps. menziesii and P. nigra var. maritima were larger than those of Will while for P. ponderosa weights were markedly smaller. Will's values for magnesium generally encompassed the range of values obtained in the present study for the Pinus species considered as a group and also for Ps. menziesii.

In comparison with the studies of Attiwill (1968) and Hatch (1955) on two Eucalyptus species, the results from the present work and that of other authors, suggests that conifers return a larger weight of elements to the forest floor than does the indigenous temperate vegetation.

Return in Australian subtropical forest is higher (Webb et al., 1969). In fact, accession of organic matter, nitrogen, phosphorus, potassium and calcium in the present study is close to that of the latter author's simple notophyll vine forest site.

Seasonal Variation in Nutrient Concentrations

Consideration of Table 5 with the aim of detecting seasonal variation in nutrient levels leads to the conclusion that a significant variation over the year of study occurred in a number of elements.

In particular, the three Pinus species were consistent in showing common seasonal peaks between October and January in their concentrations of nitrogen, iron and percentage ash. Phosphorus also showed a similar pattern in the pines with the exception of P. ponderosa. For other elements and other species no common variation of any magnitude was considered noteworthy.

The cause of this seasonal variation is of interest. It may be due to the presence of a greater than usual proportion of green foliage in the litter fall during the October/January period as this period coincides with a low in the physical weight of litter fall. Alternatively, litter collected in the traps at other periods of the year may have undergone longer periods of senescence and leaching on the tree prior to its fall. Another possibility is the deposition of aeolian dust. All of these factors probably operate to some degree.

TABLE 3. Litterfall sampling dates.

	Collection	Date	Sampling Interval (Days)
start	0 .....13. xi.	1968	0
	1 ..... 5. xii.	1968	23
	2 .....16. i.	1969	42
	3 ..... 7. v.	1969	111
	4 ..... 1. vii.	1969	55
	5 .....21. x.	1969	112
	6 .....28. i.	1970	99
	7 .....11. v.	1970	104

Table 4. Sample mean weights (g/m^2) and 95% confidence limits for physical fractions of litterfall.

	Sample	Sample size	Total litter fall	Leaf litter fall	Woody litter fall	Male cone fall	Female cone fall
P.lambertiana	1	12	24.71(29.42-20.0)	21.72(25.16-18.28)	3.23(6.01-0.45)	0.48 *	0.02 *
	2	12	17.86(22.59-13.12)	14.88(18.59-11.17)	1.96 *	2.81(4.04-1.57)	0.0 *
	3	12	143.27(178.36-108.18)	133.98(168.5-99.46)	4.95(8.04-1.85)	4.34(6.48-2.19)	0.01 *
	4	40	50.45(58.23-42.67)	40.65(44.89-36.40)	8.87(14.89-2.84)	0.20(0.28-0.12)	0.66 *
	5	40	38.76(42.55-35.03)	26.11(28.71-23.51)	12.57(14.76-10.37)	0.14(0.20-0.07)	0.04 *
	6	40	64.47(76.35-52.59)	32.52(35.85-29.20)	25.47(36.83-14.11)	6.28(7.98-4.58)	0.03 *
	7	40	413.62(439.57-387.67)	403.94(428.43-379.44)	7.27 *	0.61(0.83-0.40)	0.54 *
Ps.menziesii	1	12	32.89(38.93-26.84)	20.50(23.67-17.33)	12.13(17.11-7.14)	0.73(1.12-0.34)	0.0 *
	2	12	33.46(41.86-25.06)	26.55(29.35-23.74)	7.52(14.19-0.85)	1.16(1.90-0.43)	0.0 *
	3	12	64.47(74.59-54.36)	61.01(71.35-50.66)	3.32(5.28-1.36)	0.14(0.24-0.05)	0.0 *
	4	40	30.21(36.35-24.07)	19.90(22.21-17.60)	7.29(12.35-2.22)	0.15(0.26-0.05)	0.0 *
	5	40	36.74(40.40-33.07)	25.07(26.47-23.66)	11.53(14.88-8.17)	0.21(0.31-0.11)	0.0 *
	6	40	145.19(154.71-135.67)	124.16(130.82-117.51)	16.94(23.32-10.55)	0.11(0.16-0.05)	3.54 *
	7	40	190.49(199.57-181.41)	177.29(185.47-169.11)	11.92(17.90-5.94)	0.02 *	1.4 *
P.nigra var. maritima	1	10	40.03(46.53-33.54)	32.64(38.51-26.78)	7.08(9.91-4.26)	0.12(0.22-0.03)	0.62(1.09-0.16)
	2	10	15.81(20.69-10.92)	9.49(12.78-6.19)	5.39(7.40-3.38)	1.74(2.90-0.59)	0.14 *
	3	10	97.51(136.53-58.49)	89.86(124.86-54.90)	5.66(9.43-1.88)	1.04(1.98-0.11)	0.90(1.59-0.20)
	4	40	103.10(112.60-93.60)	95.09(103.92-86.25)	3.37(3.96-2.77)	0.25(0.33-0.17)	1.43 *
	5	40	103.86(111.96-95.75)	85.75(92.86-78.63)	17.22(20.06-14.38)	0.48(0.67-0.29)	0.47(0.68-0.26)
	6	40	78.90(97.26-60.54)	36.41(42.62-30.20)	40.36(55.90-24.83)	0.70(0.96-0.43)	1.77 *
	7	40	243.13(257.96-228.29)	224.78(239.18-210.37)	16.69(19.98-13.39)	0.21(0.31-0.11)	1.61(2.89-0.33)
P.ponderosa	1	11	24.93(31.25-18.62)	19.96(26.02-13.90)	5.40(7.82-2.98)	0.06 *	0.07 *
	2	12	35.55(66.66-4.44)	16.79(26.84-6.74)	2.73(4.04-1.41)	3.69(5.25-2.13)	14.67 *
	3	12	360.42(418.68-302.17)	337.01(388.28-285.74)	13.45(24.45-2.45)	0.95 *	8.96 *
	4	40	73.08(81.32-64.84)	68.20(75.65-60.74)	2.39(3.58-1.20)	0.52(0.86-0.18)	1.75 *
	5	40	51.46(57.06-45.86)	40.45(45.27-35.63)	10.70(13.59-7.82)	0.35(0.52-0.18)	0.07(0.13-0.02)
	6	40	78.35(87.61-69.10)	46.83(52.34-41.31)	29.31(36.15-22.46)	1.90(3.01-0.79)	0.16(0.31-0.01)
	7	40	375.77(421.07-330.46)	354.50(392.03-316.97)	13.46(16.78-10.13)	0.25(0.38-0.11)	7.29 *

TABLE 5. Estimated weights (g/m^2) of physical fractions of litterfall input to litter layers over the 365 day period from 7 May, 1969.

Species	Fraction weights				
	Total	Leaf	Wood	Male Cones	Female Cones
P. lambertiana	551.39	487.68	53.9	7.21	1.25
Ps. menziesii	395.30	339.60	47.22	0.49	4.89
P. nigra	519.64	433.38	77.00	1.63	4.82
P. ponderosa	564.20	496.34	55.34	3.01	8.99

TABLE 6. Plant nutrient status of total aerial litterfall. Sample angular means and 95% confidence limits in ppm of oven dry weight.

Element	Collection	*P. lambertiana*	*Ps. menziesii*
Nitrogen	4	7694.8 (7080.5- 8309.1)	12665.4 (11920.9-13410.0)
	5	9861.6 (9362.0-10361.3)	20219.2 (19214.5-21223.1)
	6	14649.2 (14103.1-15195.4)	9865.5 (9335.2-10395.9)
	7	5182.8 (4855.8- 5509.8)	10863.4 (10354.8-11372.6)
		P. nigra var. *maritima*	*P. ponderosa*
	4	8150.8 (7624.5- 8677.0)	11858.4 (11343.2-12373.7)
	5	9502.1 (9138.5- 9865.6)	13447.6 (12694.1-14201.2)
	6	14494.8 (13296.9-15692.7)	15082.0 (13685.4-16478.7)
	7	6440.5 (6003.1- 6877.8)	10183.3 (9130.3-11236.4)
		P. lambertiana	*Ps. menziesii*
Phosphorus	4	443.6 (401.8- 485.3)	534.5 (475.7- 593.4)
	5	592.2 (558.9- 625.5)	939.8 (876.5- 1003.1)
	6	981.7 (935.7- 1027.7)	1230.8 (1160.6- 1301.5)
	7	653.9 (608.5- 699.3)	803.4 (746.9- 860.0)

TABLE 6. Plant nutrient status of total aerial litterfall. Sample angular means and 95% confidence limits in ppm of oven dry weight. (contd.)

Element	Collection	*P. nigra* var. *maritima*	*P. ponderosa*
Phosphorus	4	280.1 (233.4- 326.7)	614.6 (583.9- 645.3)
	5	453.8 (431.1- 476.4)	746.1 (718.6- 773.7)
	6	751.6 (711.2- 792.1)	756.8 (717.5- 796.1)
	7	545.0 (511.5- 578.6)	721.2 (695.5- 746.8)
		P. lambertiana	*Ps. menziesii*
Potassium	4	827.8 (711.0- 944.5)	1248.5 (1146.3- 1350.7)
	5	1185.7 (1127.7- 1243.8)	1880.8 (1718.0- 2043.6)
	6	2675.0 (2526.9- 2823.2)	1823.9 (1699.4- 1948.5)
	7	1188.8 (1092.2- 1285.4)	1378.4 (1281.9- 1474.9)
		P. nigra var. *maritima*	*P. ponderosa*
	4	1770.1 (1628.5- 1911.7)	1892.3 (1758.4- 2026.2)
	5	1776.2 (1665.4- 1886.9)	1009.7 (939.7- 1079.8)
	6	1881.3 (1755.6- 2007.0)	2140.6 (1995.3- 2285.8)
	7	2176.8 (2052.1- 2301.6)	2598.9 (2461.2- 2736.6)

TABLE 6. Plant nutrient status of total aerial litterfall. Sample angular means and 95% confidence limits in ppm of oven dry weight. (contd.)

Element	Collection	*P. lambertiana*	*Ps. menziesii*
Calcium	4	7426.5 (6733.8- 8119.1)	10941.4 (10312.6-11570.2)
	5	7661.8 (7103.9- 8219.6)	10351.2 (9647.3-11055.1)
	6	6215.8 (5597.6- 6834.0)	11620.1 (10930.8-12309.5)
	7	8796.3 (8241.3- 9351.3)	13774.1 (12855.8-14692.4)
		P. nigra var. *maritima*	*P. ponderosa*
	4	6953.6 (6402.6- 7504.6)	3207.0 (2974.6- 3439.4)
	5	8827.3 (8166.0- 9488.7)	3430.5 (3036.4- 3824.6)
	6	7169.4 (6632.0- 7706.8)	3034.1 (2405.9- 3662.3)
	7	7016.6 (6550.6- 7482.6)	2913.2 (2673.2- 3153.1)
		P. lambertiana	*Ps. menziesii*
Magnesium	4	854.5 (780.3- 928.6)	597.7 (559.7- 635.7)
	5	655.8 (624.8- 686.8)	587.6 (558.3- 616.8)
	6	767.1 (726.8- 807.5)	756.6 (725.6- 787.7)
	7	927.9 (894.8- 961.0)	807.5 (778.6- 836.5)

TABLE 6. Plant nutrient status of total aerial litterfall. Sample angular means and 95% confidence limits in ppm of oven dry weight. (contd.)

Element	Collection	*P. nigra* var. *maritima*	*P. ponderosa*
Magnesium	4	730.5 (688.5- 772.5)	645.5 (615.2- 675.8)
	5	749.6 (698.0- 801.2)	611.7 (570.7- 652.7)
	6	788.2 (749.6- 826.7)	722.2 (665.8- 778.6)
	7	679.2 (645.1- 713.4)	647.8 (623.1- 672.6)
		P. lambertiana	*Ps. menziesii*
Manganese	4	718.1 (654.1- 782.2)	799.0 (743.5- 854.5)
	5	482.1 (442.3- 521.9)	831.3 (757.7- 904.9)
	6	454.0 (404.7- 503.3)	913.8 (841.2- 986.4)
	7	1052.0 (988.7- 1115.3)	1386.1 (1282.4- 1489.9)
		P. nigra var. *maritima*	*P. ponderosa*
	4	776.2 (708.8- 843.7)	493.8 (461.8- 525.9)
	5	1055.6 (982.1- 1129.2)	386.4 (339.7- 433.1)
	6	482.0 (427.5- 536.5)	362.9 (331.4- 394.5)
	7	834.1 (768.3- 900.0)	492.2 (467.0- 517.5)

TABLE 6. Plant nutrient status of total aerial litterfall. Sample angular means and 95% confidence limits in ppm of oven dry weight. (contd.)

Element	Collection	P. lambertiana	Ps. menziesii
Iron	4	269.7 (221.9- 317.5)	834.0 (782.2- 885.9)
	5	862.8 (768.0- 957.5)	1658.1 (1531.8- 1784.5)
	6	2125.4 (1914.7- 2336.0)	1367.5 (1276.1- 1459.0)
	7	181.0 (138.2- 223.8)	553.2 (487.8- 618.6)
		P. nigra var. maritima	P. ponderosa
	4	526.2 (473.5- 578.9)	336.5 (315.0- 358.0)
	5	585.3 (554.5- 616.0)	690.4 (574.3- 806.5)
	6	2844.3 (2466.1- 3222.6)	2272.8 (2054.6- 2491.1)
	7	608.2 (489.1- 727.4)	147.9 (105.8- 190.1)
		P. lambertiana	Ps. menziesii
Zinc	4	17.3 (14.4- 20.3)	21.9 (17.3- 26.6)
	5	22.0 (20.1- 23.9)	15.2 (12.6- 17.8)
	6	46.0 (41.8- 50.2)	13.9 (12.0- 15.8)
	7	42.3 (39.7- 44.8)	20.3 (18.6- 22.1)

TABLE 6. Plant nutrient status of total aerial litterfall. Sample angular means and 95% confidence limits in ppm of oven dry weight. (contd.)

Element	Collection	*P. nigra* var. *maritima*	*P. ponderosa*
Zinc	4	16.7 (12.9- 20.5)	21.2 (13.2- 29.2)
	5	56.6 (52.9- 60.3)	22.1 (20.1- 24.2)
	6	23.9 (21.1- 26.8)	22.4 (19.9- 24.8)
	7	23.1 (21.2- 25.0)	35.9 (33.7- 38.1)
		P. lambertiana	*Ps. menziesii*
% Ash	4	2.755 (2.519- 2.991)	6.673 (6.161- 7.186)
	5	3.625 (3.457- 3.792)	7.767 (7.270- 8.265)
	6	7.551 (6.972- 8.130)	7.812 (7.405- 8.219)
	7	3.902 (3.673- 4.131)	8.102 (7.711- 8.493)
		P. nigra var. *maritima*	*P. ponderosa*
	4	3.303 (3.113- 3.494)	2.553 (2.344- 2.761)
	5	4.312 (4.093- 4.530)	3.812 (3.647- 3.977)
	6	10.077 (9.410- 10.743)	6.620 (6.175- 7.064)
	7	3.811 (3.577- 4.044)	2.253 (2.141- 2.366)

Sample	Elemental Weights								
	N	P	K	Ca	Mg	Mn	Fe	Zn	Ash
P. lambertiana									
4	0.3882	0.0224	0.0418	0.3747	0.0431	0.0362	0.0136	0.0009	1.3899
5	0.3822	0.0229	0.0460	0.2969	0.0254	0.0187	0.0334	0.0009	1.4050
6	0.9444	0.0633	0.1724	0.4007	0.0494	0.0293	0.1370	0.0030	2.5156
7	2.1434	0.2705	0.4917	3.6382	0.3837	0.4351	0.0740	0.0174	16.1394
Annual	3.7758	0.3687	0.7330	4.5706	0.4868	0.5027	0.2551	0.0215	20.8291
Ps. menziesii									
4	0.3826	0.0161	0.0376	0.3296	0.0180	0.0250	0.0251	0.0006	2.0159
5	0.7429	0.0345	0.0691	0.3803	0.0216	0.0305	0.0609	0.0006	2.8536
6	1.4324	0.1787	0.2648	1.6871	0.1098	0.1327	0.1985	0.0020	11.3422
7	2.0694	0.1530	0.2626	2.6238	0.1538	0.2640	0.1054	0.0039	15.4335
Annual	4.5477	0.3764	0.6240	4.9199	0.2973	0.4420	0.3858	0.0063	31.0516
P. nigra var. maritima									
4	0.8403	0.0289	0.1825	0.7169	0.0753	0.0800	0.0542	0.0017	3.4054
5	0.9869	0.0471	0.1844	0.9168	0.0778	0.1096	0.0608	0.0058	4.4784
6	1.1436	0.0593	0.1484	0.5657	0.0622	0.0380	0.2244	0.0019	7.9507
7	1.5659	0.1325	0.5292	1.7059	0.1651	0.2028	0.1479	0.0056	9.2657
Annual	4.4764	0.2627	1.0242	3.8397	0.3741	0.4226	0.4816	0.0148	24.7438
P. ponderosa									
4	0.8666	0.0449	0.1383	0.2344	0.0472	0.0361	0.0246	0.0015	1.8657
5	0.6920	0.0385	0.0521	0.1769	0.0315	0.0199	0.0356	0.0011	1.9616
6	1.1817	0.0593	0.1677	0.2377	0.0566	0.0284	0.1781	0.0018	5.1868
7	3.8266	0.2710	0.9766	1.0947	0.2434	0.1850	0.0556	0.0134	8.4661
Annual	6.4197	0.4033	1.2971	1.7016	0.3694	0.2622	0.2918	0.0173	17.1546

Table 7. Mean weight of plant nutrient elements in g/m^2 added to litter layers from aerial litterfall over each sample period.

PERCENTAGE ASH

P. lambertiana	Ps. menziesii	P. nigra	P. ponderosa	Collection 4	Collection 5	Collection 6	Collection 7
6	7	6 (a)	6	M	M	N	M
7	6	5	5	N	N	M	L
5	5	7	4	L	P	L	N
4	4	4	7	P	L	P	P

RATE OF ASH FALL

P. lambertiana	Ps. menziesii	P. nigra	P. ponderosa	Collection 4	Collection 5	Collection 6	Collection 7
7 (a)	7 (a)	7 (a)	7 (a)	M	N (a)	N (a)	L
4	4	6	6	P	P	P	M
5	6	5	4	L	L	M	N
6	5	4	5	N	M	L	P

(a) denotes all means significantly different at $P < 0.05$

Table 8. Non-parametric STP analysis of litterfall sample ash values. Vertical lines denote non-significant subsets ($P<0.05$). Samples listed in decreasing order of mean.

TABLE 9. Canonical variate analysis of litterfall. Significant ($P < 0.05$) eigenvalues and percentages of total variability exhibited by each.

Species	Order	Eigenvalue	Percentage	Cumulative Percentage
Rate of Fall Analysis				
P. *lambertiana*	1	16.6831	90.6365	90.6365
	2	1.5304	8.3142	98.9507
	3	0.1932	1.0495	100.0000
Ps. *menziesii*	1	25.4832	91.7826	91.7826
	2	2.2801	8.2124	99.9950
P. *nigra* var. *maritima*	1	9.7161	60.8481	60.8481
	2	4.1247	25.8316	86.6797
	3	2.1269	13.3203	100.0000
P. *ponderosa*	1	8.6289	82.9079	82.9079
	2	1.2697	12.1993	95.1072
	3	0.5092	4.8928	100.0000
Combined Analysis	1	10.3228	45.0006	45.0006
	2	5.0553	22.0379	67.0385
	3	3.6665	15.9834	83.0219
	4	1.9182	8.3622	91.3841

TABLE 9. Canonical variate analysis of litterfall. Significant ($P < 0.05$) eigenvalues and percentages of total variability exhibited by each. (contd.)

Species	Order	Eigenvalue	Percentage	Cumulative Percentage
Concentration Analysis				
P. *lambertiana*	1	11.9991	74.3387	74.3387
	2	3.8052	23.5747	97.9134
	3	0.3368	2.0867	100.0000
Ps. *menziesii*	1	9.8793	65.6675	65.6675
	2	4.6008	30.5813	97.2488
	3	0.5644	3.7513	100.0000
P. *nigra* var. *maritima*	1	6.9019	60.9775	60.9775
	2	3.1099	27.4755	88.4530
	3	1.3070	11.5471	100.0000
P. *ponderosa*	1	6.7993	68.3578	68.3578
	2	2.6025	26.1648	94.5226
	3	0.5448	5.4774	100.0000
Combined Analysis	1	5.8976	33.5365	33.5365
	2	4.6477	26.4290	59.9655
	3	2.4589	13.9824	73.9479
	4	2.0321	11.5555	85.5034
	5	1.2340	7.0171	92.5205
	6	0.9073	5.1594	97.6799

Species	Root	N	P	K	Ca	Mg	Mn	Fe	Zn
Rate of Fall Analysis									
	1	0.0978	0.0349	0.0351	0.0504	0.6285	-0.0936	-0.1766	-0.7419
	2	0.0581	-0.0093	-0.0383	0.0115	0.0383	-0.0858	-0.0734	-0.9863
P. lambertiana	3	-0.0017	-0.0589	-0.0097	-0.0087	0.2174	-0.0354	-0.1501	-0.9619
	1	0.0158	-0.0111	0.0032	0.0050	0.0427	0.0127	-0.0101	-0.9988
Ps. menziesii	2	0.0580	-0.1531	0.0138	0.0156	-0.4135	-0.0778	0.0638	0.8897
	1	-0.0165	-0.0650	0.1117	0.0054	0.0343	0.0622	-0.0113	-0.9888
	2	0.0586	0.1011	-0.0708	0.0055	-0.0116	-0.1050	-0.0009	-0.9850
P. nigra var. maritima	3	-0.0065	0.0659	0.0092	-0.0015	0.0214	-0.0224	0.0108	-0.9972
	1	0.0212	-0.2633	0.1193	-0.0005	0.0439	0.0553	-0.1594	0.9411
	2	0.0157	0.2876	-0.2341	-0.0377	0.0889	0.3152	-0.5151	-0.6987
P. ponderosa	3	0.0340	-0.3156	0.0181	-0.0041	0.1664	0.0146	-0.0304	-0.9328
Concentration Analysis									
	1	0.0409	-0.1735	0.1746	0.0188	-0.2596	-0.2024	0.1874	0.8910
	2	-0.0153	0.0992	0.0276	-0.0051	-0.0149	0.0732	0.0151	0.9916
P. lambertiana	3	0.0547	-0.6709	0.1184	-0.0497	0.6358	-0.2281	-0.0660	0.2643
	1	0.0832	-0.4127	0.0664	0.0094	-0.7274	-0.1820	0.0714	0.5009
	2	-0.0066	0.0821	0.0170	-0.0029	-0.0979	-0.0071	0.0515	0.9903
Ps. menziesii	3	-0.0180	-0.0747	0.0016	-0.0012	-0.1047	-0.1701	0.0164	0.9767
	1	0.0236	0.4567	-0.0925	0.0129	0.2187	-0.2146	0.0766	-0.8261
	2	-0.0035	-0.0031	0.0100	-0.0019	0.0027	-0.0097	0.0021	-0.9999
P. nigra var. maritima	3	-0.0257	0.3732	0.0620	0.0075	-0.1772	0.0148	0.0056	0.9080
	1	0.0025	0.1281	-0.0646	0.0161	-0.0047	-0.2842	0.1696	-0.9352
	2	-0.0043	-0.3005	0.2550	-0.0127	-0.0173	-0.0250	0.0806	0.9149
P. ponderosa	3	0.0088	-0.3072	0.0023	-0.0070	0.0655	0.0701	-0.0018	-0.9467

Table 10. Canonical variate analysis of litterfall. Intra species analysis. Normalised coefficients for each significant discriminant function.

Species	Root	N	P	K	Ca	Mg	Mn	Fe	Zn
Rate of Fall Analysis									
	1	0.1614	0.0140	0.0259	0.1226	0.2663	-0.0544	-0.0620	-0.0228
	2	0.0959	-0.0360	-0.0283	0.0279	0.0162	-0.0498	-0.0258	-0.0303
P. lambertiana	3	-0.0027	-0.0237	-0.0071	-0.0211	0.0921	-0.0206	-0.0527	-0.0295
	1	0.0199	-0.0026	0.0013	0.0082	0.0080	0.0047	-0.0026	-0.0131
	2	0.0731	-0.0363	0.0055	0.0256	-0.0771	-0.0292	0.0162	0.0116
Ps. menziesii									
	1	-0.0305	-0.0173	0.0727	0.0121	0.0120	0.0266	-0.0092	-0.0201
	2	0.1085	0.0269	-0.0461	0.0124	-0.0040	-0.0449	-0.0008	-0.0201
P. nigra var. maritima	3	-0.0121	0.0175	0.0060	-0.0035	0.0075	-0.0096	0.0088	-0.0205
	1	0.0613	-0.1389	0.1540	-0.0009	0.0217	0.0215	-0.0951	0.0380
	2	0.0453	0.1518	-0.3024	-0.0675	0.0440	0.1226	-0.3075	-0.0282
P. ponderosa	3	0.0983	-0.1665	0.0234	-0.0073	0.0823	0.0057	-0.0182	-0.0377
Concentration Analysis									
	1	0.1656	-0.0791	0.1997	0.1074	-0.1342	-0.1210	0.2317	0.0302
	2	-0.0621	0.0452	0.0316	-0.0292	-0.0077	0.0438	0.0187	0.0336
P. lambertiana	3	0.2215	-0.3058	0.1354	-0.2836	0.3285	0.1364	-0.0816	0.0090
	1	0.4403	-0.2764	0.0854	0.0532	-0.2518	-0.1519	0.0776	0.0164
	2	-0.0348	0.0550	0.0219	-0.0167	-0.0339	-0.0059	0.0560	-0.0324
Ps. menziesii	3	-0.0954	-0.0500	0.0021	-0.0066	-0.0562	-0.1420	0.0178	0.0320
	1	0.1280	0.1850	-0.1201	0.0593	-0.0998	-0.1522	0.1527	-0.0295
	2	-0.0191	-0.0013	0.0130	-0.0087	0.0012	-0.0069	0.0041	-0.0357
P. nigra var. maritima	3	-0.1391	0.1512	0.0805	0.0343	-0.0809	0.0105	0.0111	0.0325
	1	0.0176	0.0435	-0.0837	0.0623	-0.0020	-0.1090	0.2218	-0.0465
	2	-0.0297	-0.1021	0.3300	-0.0492	-0.0076	0.0096	0.1054	0.0456
P. ponderosa	3	0.0611	-0.1044	0.0030	-0.0273	0.0286	0.0269	-0.0024	-0.0472

Table 11. Canonical variate analysis of litterfall. Intra species analysis. Scaled coefficients for all significant discriminant functions.

TABLE 12. Plant nutrient concentration analysis of litterfall. Maximal acceptable combinations of variables and samples using maximum characteristic root STP at $P < 0.05$ level. Inter-species analysis of each sampling interval.

Variable Combinations	Sample Combinations
i. *Pinus lambertiana*	
P, K, Ca	5, 7
P, Ca, Zn	4, 5
K, Ca, Zn	4, 5
K, Mg, Fe	4, 7
Ca, Mg, Fe	4, 7
Ca, Mg	4, 6
Ca, Mn	5, 6
Mg, Mn	5, 6
Zn	6, 7
ii. *Pseudotsuga menziesii*	
K, Ca, Mn, Zn	5, 6
K, Ca, Fe, Zn	5, 6
K, Mg, Fe, Zn	5, 6
Ca, Mg, Mn, Zn	4, 5
N, K, Zn	4, 7
N, Ca, Mg	6, 7
N, Ca, Zn	6, 7
N, Mg, Zn	6, 7
N, Fe, Zn	4, 7
K, Fe, Zn	4, 7
Ca, Mg, Zn	6, 7
Ca, Mn, Zn	4, 5, 6
P, Zn	5, 7
Ca, Zn	4, 7
iii. *Pinus nigra* var. *maritima*	
N, Ca, Mg, Mn, Fe	4, 7
N, Ca, Mg, Mn, Zn	4, 7
N, Ca, Mn, Fe, Zn	4, 7
K, Ca, Mg, Mn, Fe	4, 7
Ca, Mg, Mn, Fe, Zn	4, 7
N, K, Mg, Fe	4, 5
K, Ca, Mg, Fe	4, 5
K, Ca, Mg, Fe	4, 6
K, Ca, Mg, Zn	6, 7
K, Ca, Fe, Zn	4, 7
P, K, Fe	5, 7
P, Mg, Fe	5, 7
K, Ca, Mg	5, 6
K, Ca, Mg	5, 7
K, Ca, Zn	4, 6
K, Mg, Fe	5, 7
Ca, Mg, Fe	5, 7
Ca, Mg, Zn	4, 6, 7
K, Ca	4, 5, 6
K, Mg	4, 5, 6

TABLE 12. Plant nutrient concentration analysis of litterfall. Maximal acceptable combinations of variables and samples using maximum characteristic root STP at P <0.05 level. Inter-species analysis of each sampling interval. (contd.)

Variable Combinations	Sample Combinations
iii. Pinus nigra var. maritima (contd.)	
K, Fe	4, 5, 7
Ca, Mg	5, 6, 7
Mg, Fe	4, 5, 7
Mn, Fe	5, 7
iv. Pinus ponderosa	
N, P, Ca, Mn, Zn	5, 6
N, Ca, Mg, Mn, Fe	4, 7
N, P, Mg, Zn	5, 6
N, K, Ca, Zn	4, 6
N, Ca, Mg, Mn	4, 7
N, Ca, Mg, Fe	4, 7
N, Ca, Mg, Zn	4, 5
N, Ca, Mn, Fe	4, 7
N, Ca, Fe, Zn	5, 6
N, Mg, Mn, Fe	4, 7
N, Mg, Fe, Zn	4, 5
P, Ca, Mg, Mn	4, 7
K, Ca, Mg, Zn	4, 6
Ca, Mg, Mn, Fe	4, 7
Ca, Mg, Mn, Zn	4, 5
Ca, Mg, Mn, Zn	4, 7
N, Ca, Fe	4, 5
N, Ca, Zn	4, 5, 6
N, Mg, Zn	4, 6
P, Ca, Mg	5, 7
P, Ca, Mg	6, 7
P, Ca, Zn	5, 7
P, Ca, Zn	6, 7
P, Mg, Mn	5, 7
P, Mg, Zn	5, 6
P, Mg, Zn	5, 7
Ca, Mg, Zn	5, 7
Ca, Mn, Zn	4, 7
Ca, Fe, Zn	4, 5
N, Mg	4, 5, 7
N, Mn	4, 5
P, Ca	5, 6, 7
P, Mg	5, 6, 7
P, Zn	5, 6, 7
K, Ca	6, 7
Ca, Mg	4, 5, 7
Ca, Mg	4, 6, 7
Ca, Zn	4, 6, 7
Ca, Zn	5, 6, 7
Mg, Mn	4, 5, 7
Mg, Zn	4, 5, 6
Mg, Zn	4, 5, 7
Mg, Zn	5, 6, 7
Ca	4, 5, 6, 7

TABLE 13. Plant nutrient rate of fall analysis of litterfall. Maximal acceptable combinations of variables and samples using maximum characteristic root STP at $P < 0.05$. Inter-species analysis of each sampling interval.

Variable Combination	Sample Combination
(i) Collection Interval Four	
N, Ca, Mg, Mn, Zn	L, N
N, P, Mg, Zn	M, P
P, Ca, Zn	L, N
P, Mn, Zn	L, M
K, Mg, Zn	N, P
Mg, Mn, Zn	M, N
P, K	L, M
K, Zn	L, M
Mg, Zn	M, N, P
Mn, Zn	L, M, N
Fe, Zn	L, P
Zn	L, M, N, P
(ii) Collection Interval Five	
K, Mg, Mn, Fe, Zn	L, P
N, Ca, Mg	L, N
N, Ca, Fe	L, N
K, Ca	M, N
Mg, Zn	L, M, P
Fe	N, P
(iii) Collection Interval Six	
N, P, Mg, Mn, Fe, Zn	N, P
N, P, K, Mn, Zn	N, P
N, P, K, Fe, Zn	N, P
N, Ca, Mg, Mn	L, N
N, Ca, Mn, Fe	L, N
N, Mg, Mn, Fe	L, N
N, Mg, Mn, Fe	L, P
N, Mg, Mn	L, N, P
N, Mg, Fe	L, N, P
N, Mn, Fe	L, N, P
K, Mg, Zn	M, N

TABLE 13. Plant nutrient rate of fall analysis of litterfall. Maximal acceptable combinations of variables and samples using maximum characteristic root STP at $P < 0.05$. Inter-species analysis of each sampling interval. (contd.)

Variable Combination	Sample Combination
(iii) Collection Interval Six (contd.)	
Mg, Mn, Fe	L, N, P
K, Mg	M, P
K, Zn	[illegible], N, P
Mg, Fe	L, M
Mg, Zn	M, N, P
Mg	L, M, N, P
(iv) Collection Interval Seven	
P, Mg, Fe, Zn	M, N
N, P, Mn	M, N
N, Ca, Fe	L, M
P, K, Fe	M, N
N, Ca	M, N
P, Fe	L, P
K, Fe	L, N
Mn, Fe	M, [illegible]
Fe, Zn	L, P
Mn	N, P
Zn	N, P

TABLE 14. Rate of fall of plant nutrient elements in total litterfall over collection intervals four to seven. Maximal acceptable combinations of variables and samples using maximum characteristic root STP at P <0.05 level. Intra species temporal analysis.

Variable Combinations	Sample Combinations
(i) Pinus lambertiana	
P, K, Mg, Mn, Fe	5, 6
P, K, Mg, Mn, Zn	5, 6
P, K, Mn, Fe, Zn	4, 5
K, Mg, Mn, Fe, Zn	5, 6
P, Ca, Mg	5, 6
Ca, Mg, Zn	5, 6
K, Zn	4, 5, 6
Fe, Zn	4, 5, 6
(ii) Pseudotsuga menziesii	
N, P, K, Ca, Mg, Mn, Fe, Zn	5, 6
(iii) Pinus nigra var. maritima	
K, Ca, Mg	5, 6
N, P	5, 6
N, Mg	5, 6
Fe, Zn	5, 7
(iv) Pinus ponderosa	
N, P, K, Ca, Mg, Zn	4, 7
N, P, K, Ca, Mg	4, 6
N, P, K, Ca, Zn	4, 6
N, P, K, Mg, Zn	4, 6
N, P, Ca, Mg, Zn	4, 6
N, K, Ca, Mg, Zn	4, 6
P, K, Ca, Mg, Zn	4, 6
P, K, Mg, Mn, Zn	5, 6
N, K, Ca, Mn	4, 6
P, Ca, Mn, Zn	5, 6
K, Ca, Mg, Zn	5, 6
Ca, Mg, Mn, Zn	5, 6
P, Ca, Mg	5, 6
P, Fe, Zn	4, 5
P, Zn	4, 5, 6
Fe	4, 5, 7

TABLE 15. Rate of fall of plant nutrient elements in total litterfall over collection intervals four to seven. Maximal acceptable combinations of variables and samples using maximum characteristic root STP at P <0.05 per cent level. Intra species temporal analysis.

Variable combination	Sample Combination
(i) Interval Four	
N, P, K, Zn	L, M
N, K, Ca, Zn	L, M
P, K, Ca, Zn	L, M
P, K, Mn, Zn	L, M
N, K, Fe	L, M
N, Fe, Zn	L, M
K, Fe, Zn	L, M
Mg, Mn, Fe	L, P
Mg, Mn, Zn	L, P
Mg, Fe, Zn	L, P
Ca, Mn	L, M
Ca, Fe	M, P
Mn, Zn	L, M, P
Fe, Zn	L, M, P
(ii) Interval Five	
K, Mg, Mn, Fe, Zn	L, P
Ca, Mn, Fe	L, P
Mn, Zn	L, M
Mn, Zn	M, P
(iii) Interval Six	
N, P, K, Ca, Mg, Mn, Fe, Zn	L, M
N, P, Mg, Fe, Zn	N, P
N, P, Mg, Fe	L, P
Mg, Mn, Fe, Zn	N, P
N, P, K	N, P
N, K, Zn	N, P
N, Mg, Mn	N, P
N, Mn, Zn	N, P
P, K, Zn	N, P
P, Mn	N, P
K, Fe	N, P
(iv) Interval Seven	
P, Mg, Fe, Zn	M, N
N, P, Mn	M, N
N, Ca, Fe	L, M
P, Mn, Fe	M, N
P, Fe	L, P
K, Fe	L, N
Mn, Fe	M, N
Fe, Zn	L, P
Mn	N, P

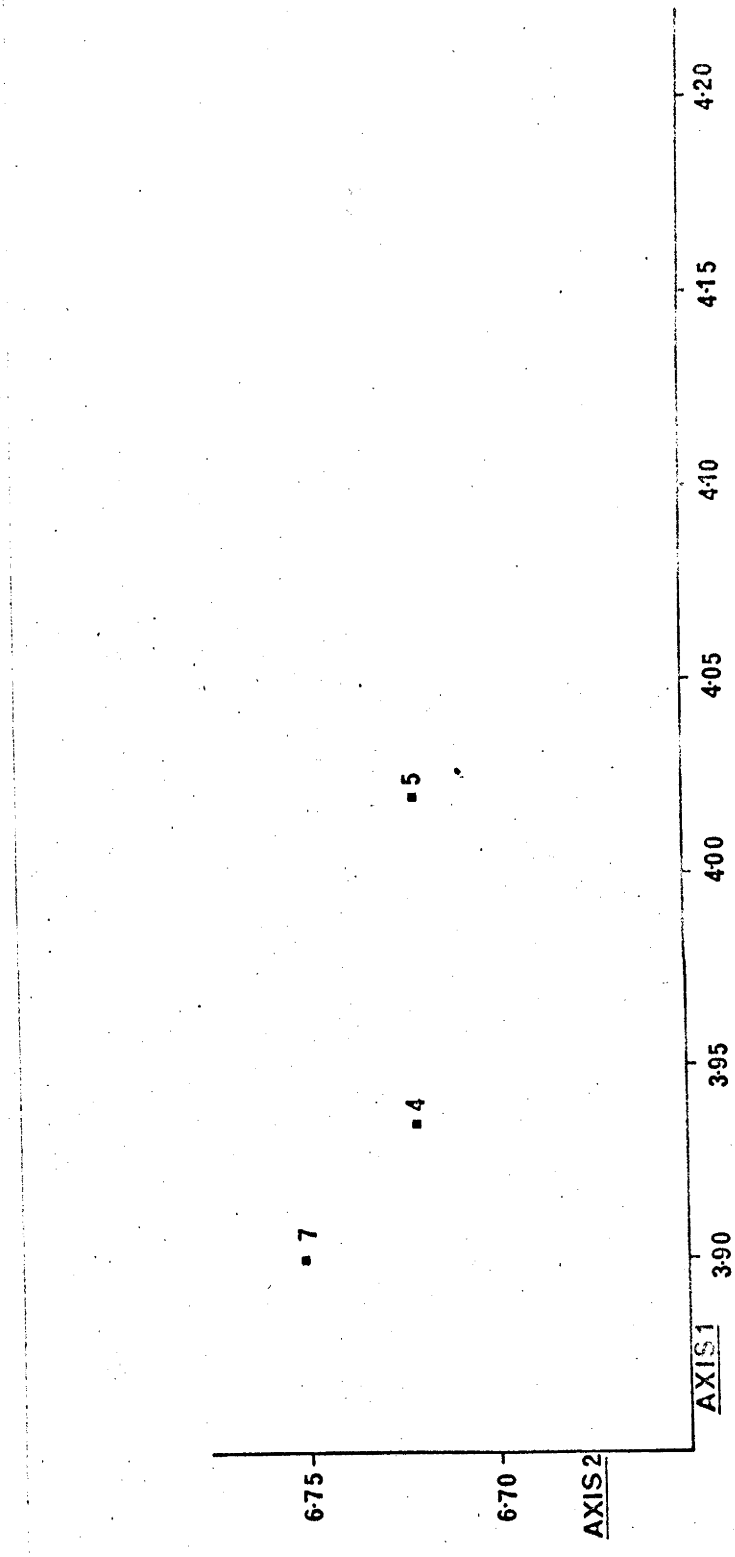

Fig. 2. Pinus lambertiana. Litterfall plant nutrient concentration analysis of samples 4 to 7. Mean canonical points.

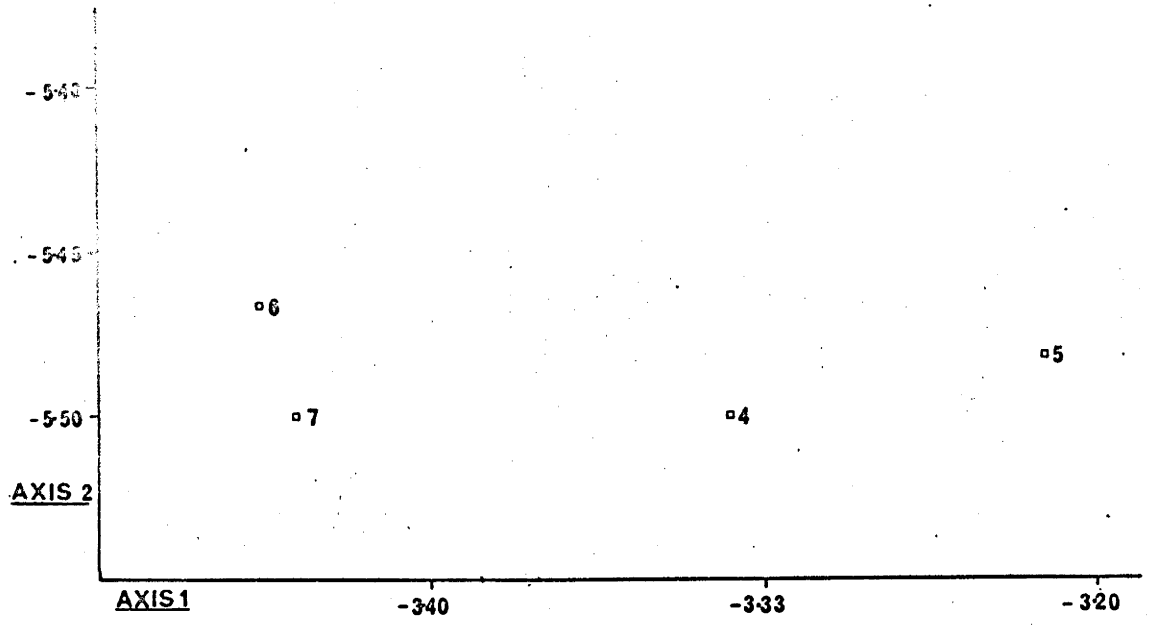

Fig. 3. Pseudotsuga menziesii. Litterfall plant nutrient concentration analysis of samples 4 to 7. Mean canonical points.

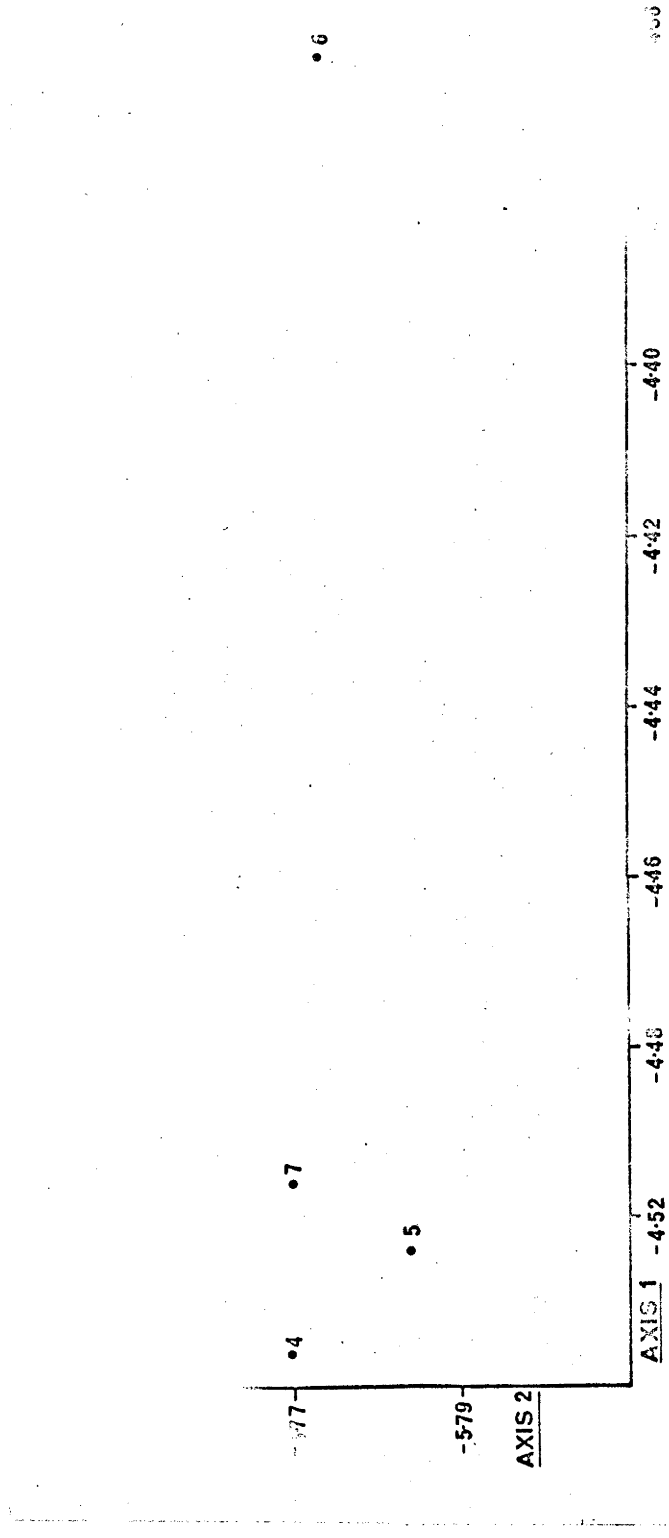

Fig. 4(a). Axes 1 and 2. Pinus nigra var. maritima. Litterfall plant nutrient concentration analysis of samples 4 to 7. Mean canonical points.

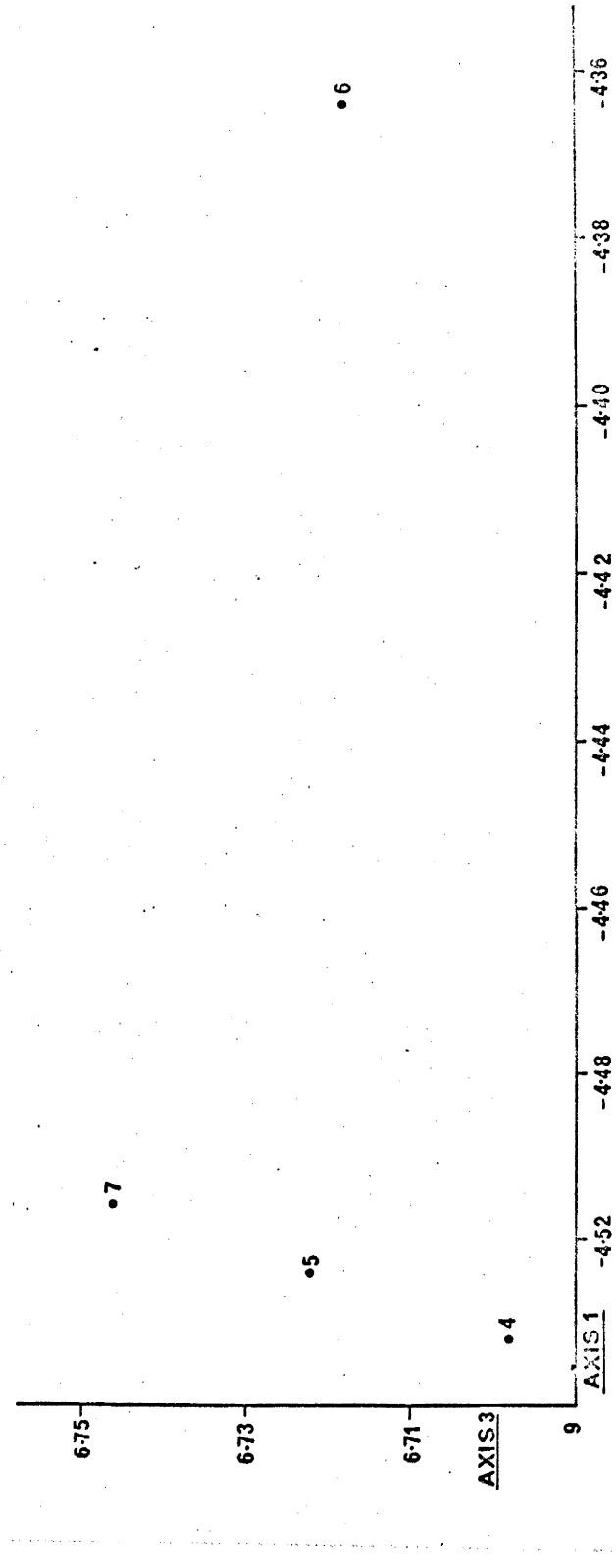

Fig. 4(b). Axes 1 and 3. Pinus nigra var. maritima. Litterfall plant nutrient concentration analysis of samples 4 to 7. Mean canonical points.

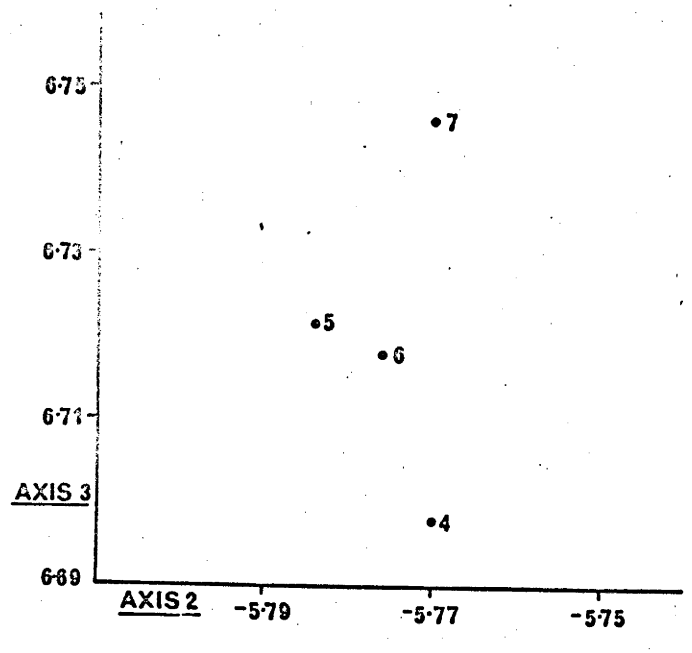

Fig. 4(c). Axes 2 and 3. Pinus nigra var. maritima. Litterfall plant nutrient concentration analysis of samples 4 to 7. Mean canonical points.

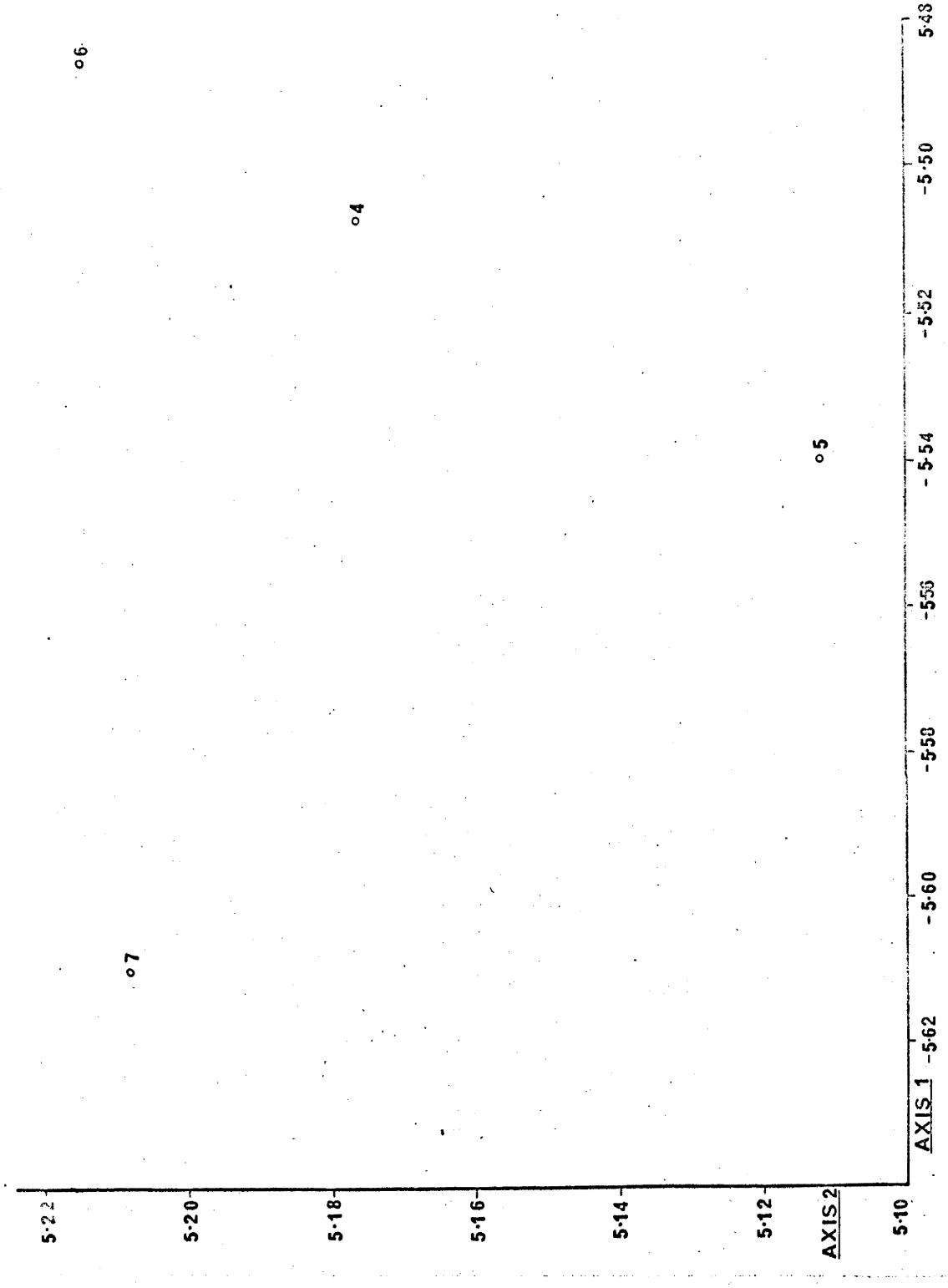

Fig. 5(a). Axes 1 and 2. Pinus ponderosa. Litterfall plant nutrient concentration analysis. Mean canonical points.

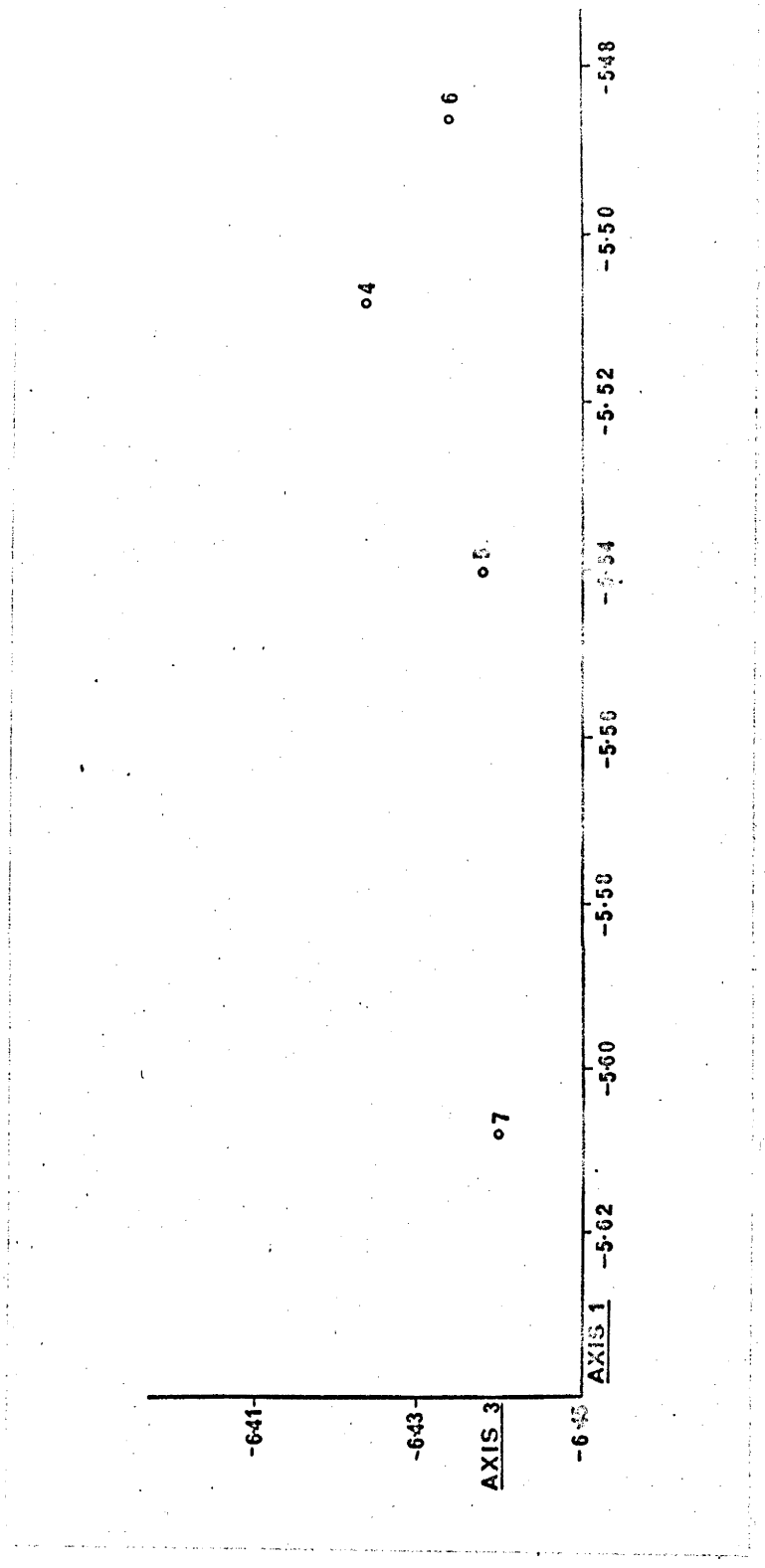

Fig. 5(b). Axes 1 and 3. Pinus ponderosa. Litterfall plant nutrient concentration analysis. Mean canonical points.

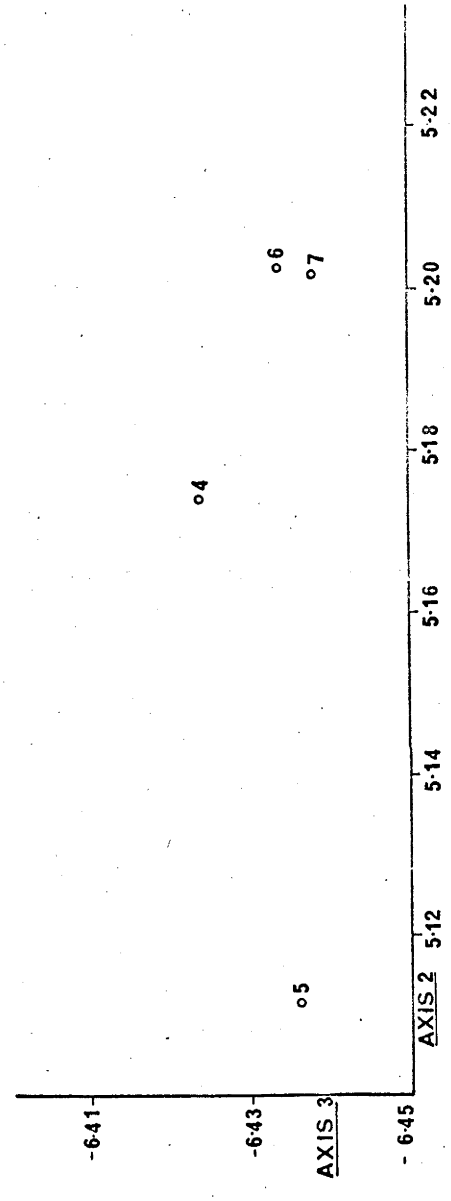

Fig. 5(c). Axes 2 and 3. Pinus ponderosa. Litterfall plant nutrient concentration analysis. Mean canonical points.

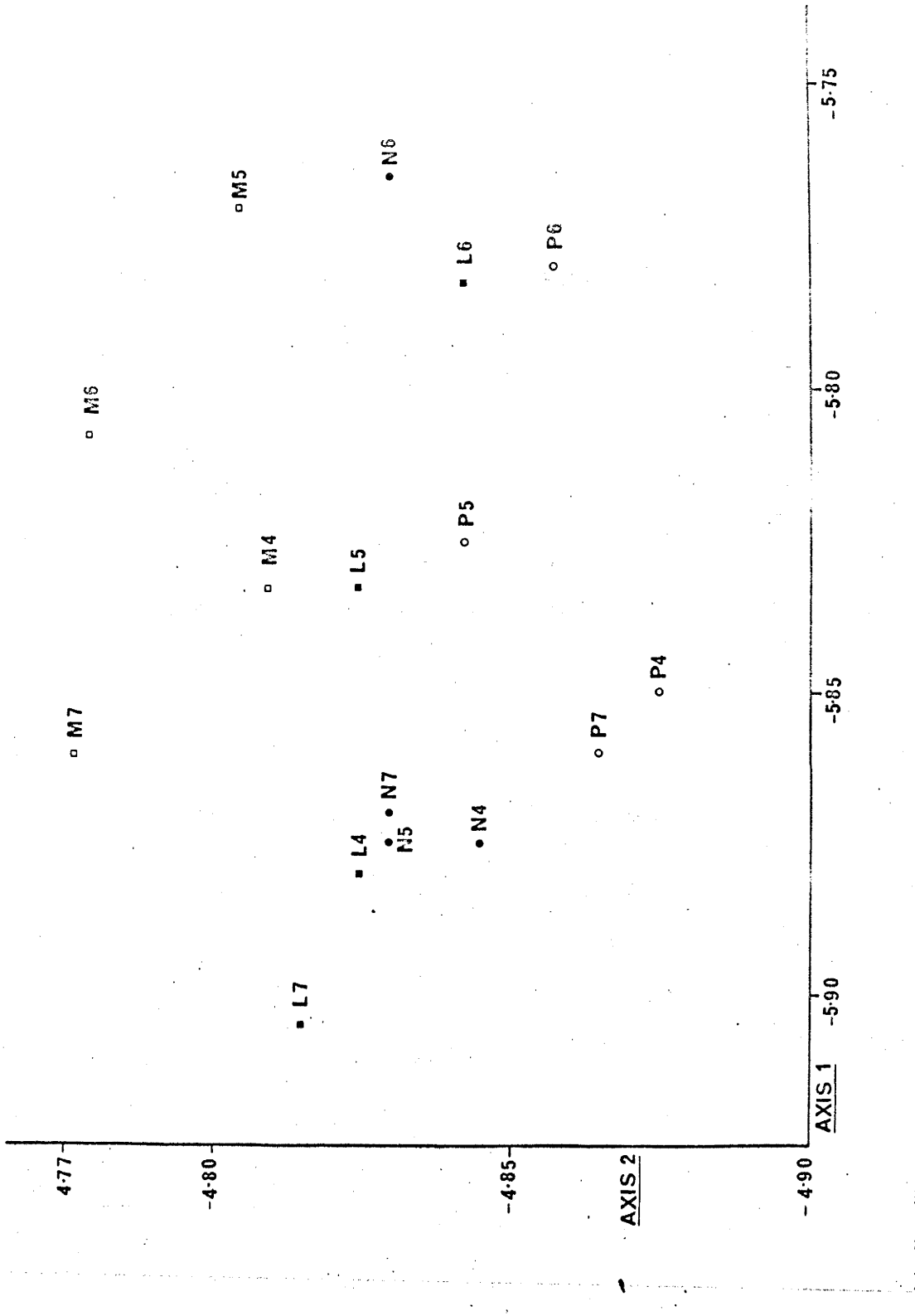

Fig. 6(a). Axes 1 and 2. Combined litterfall plant nutrient concentration analysis. Mean canonical points.

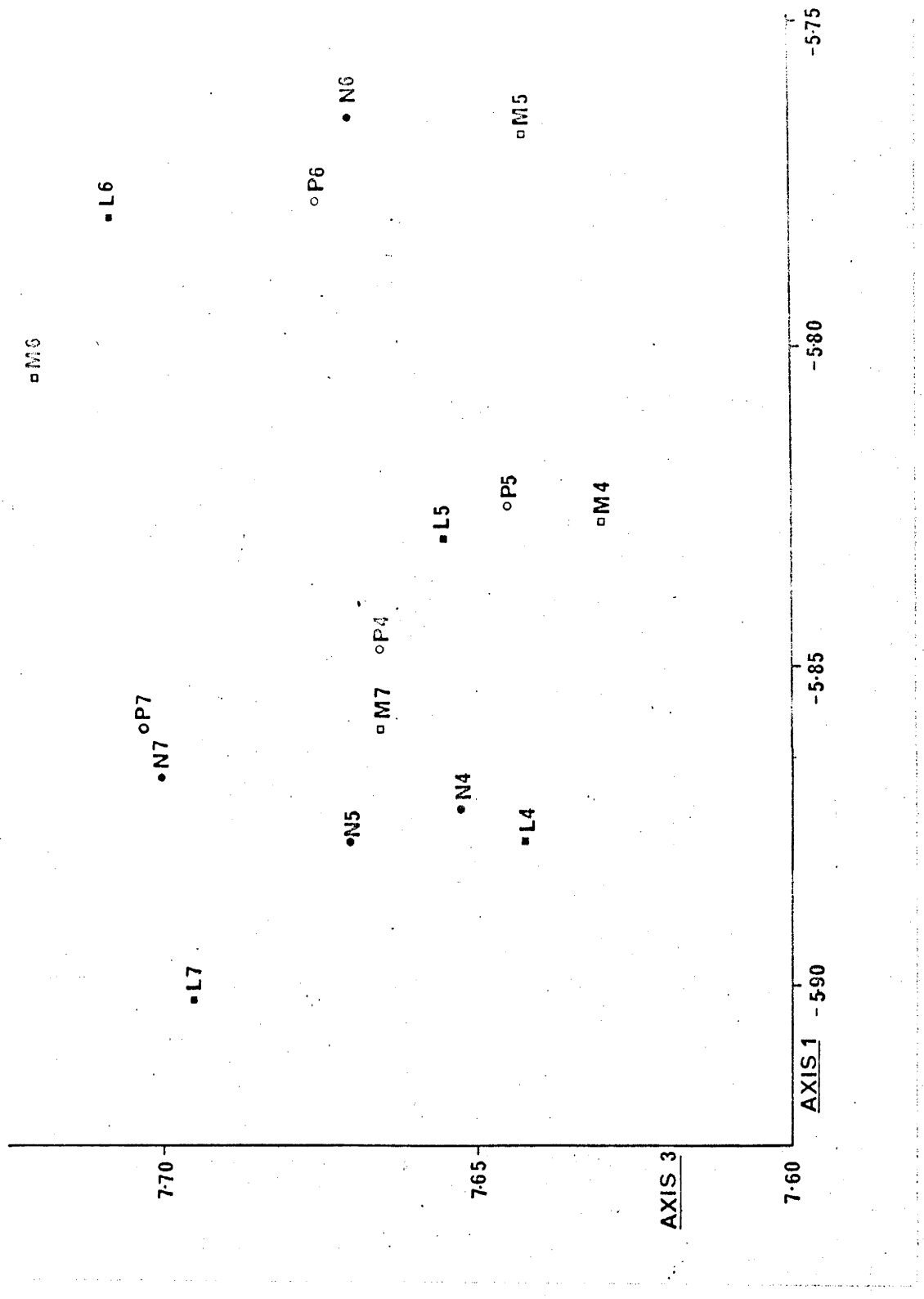

Fig. 6(b). Axes 1 and 3. Combined litterfall plant nutrient concentration analysis. Mean canonical points.

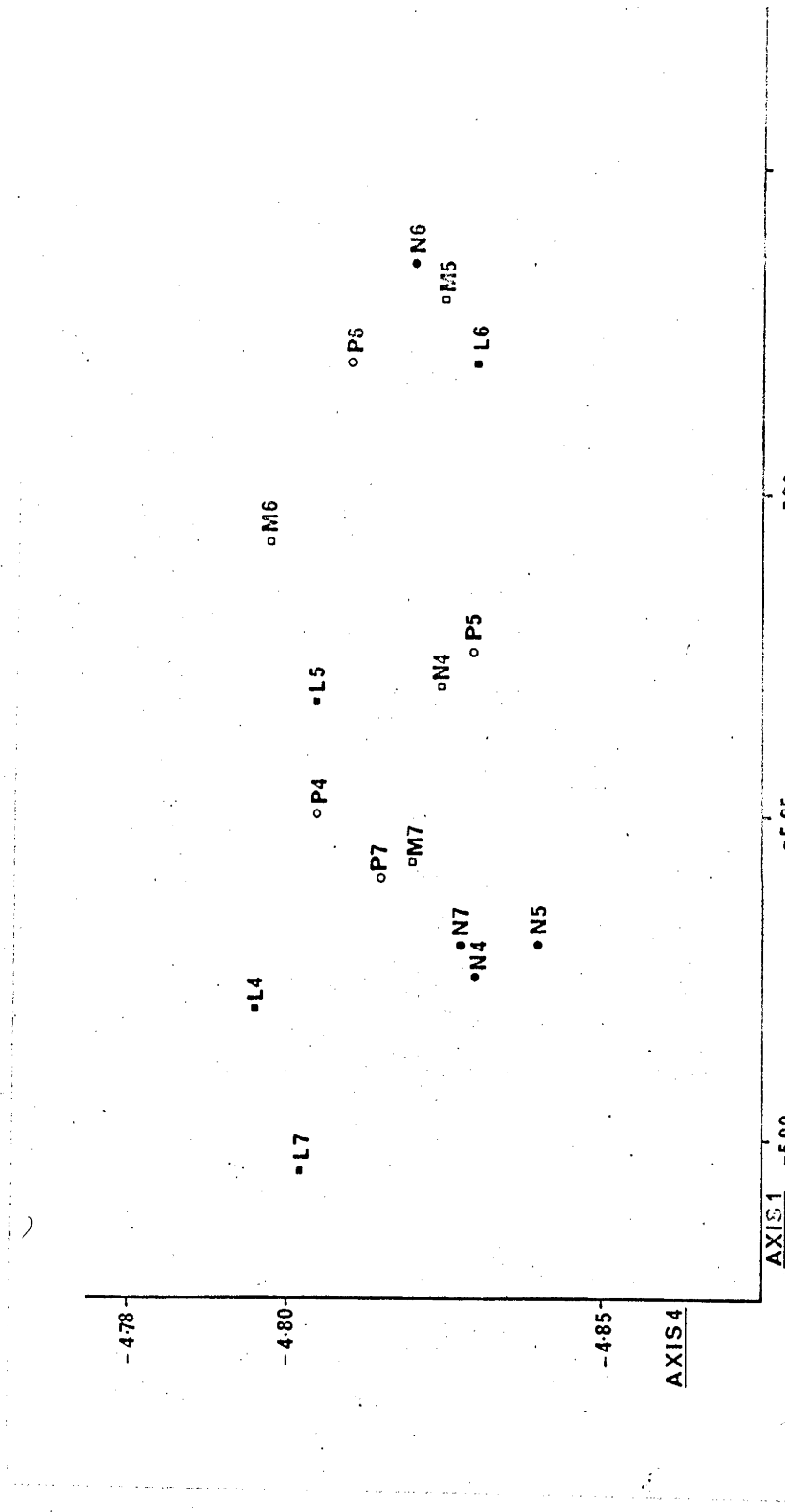

Fig. 6(c). Axes 1 and 4. Combined litterfall plant nutrient concentration analysis. Mean canonical points.

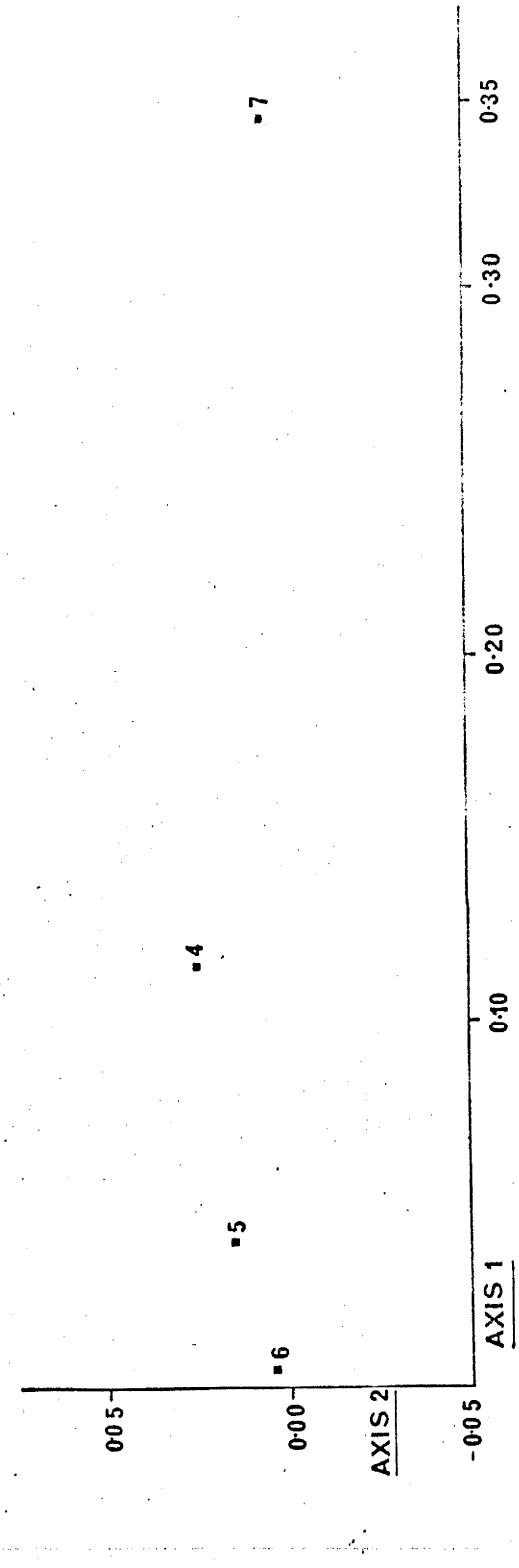

Fig. 7. Pinus lambertiana. Analysis of rate of fall of selected plant nutrient elements for samples 4 to 7. Mean canonical points.

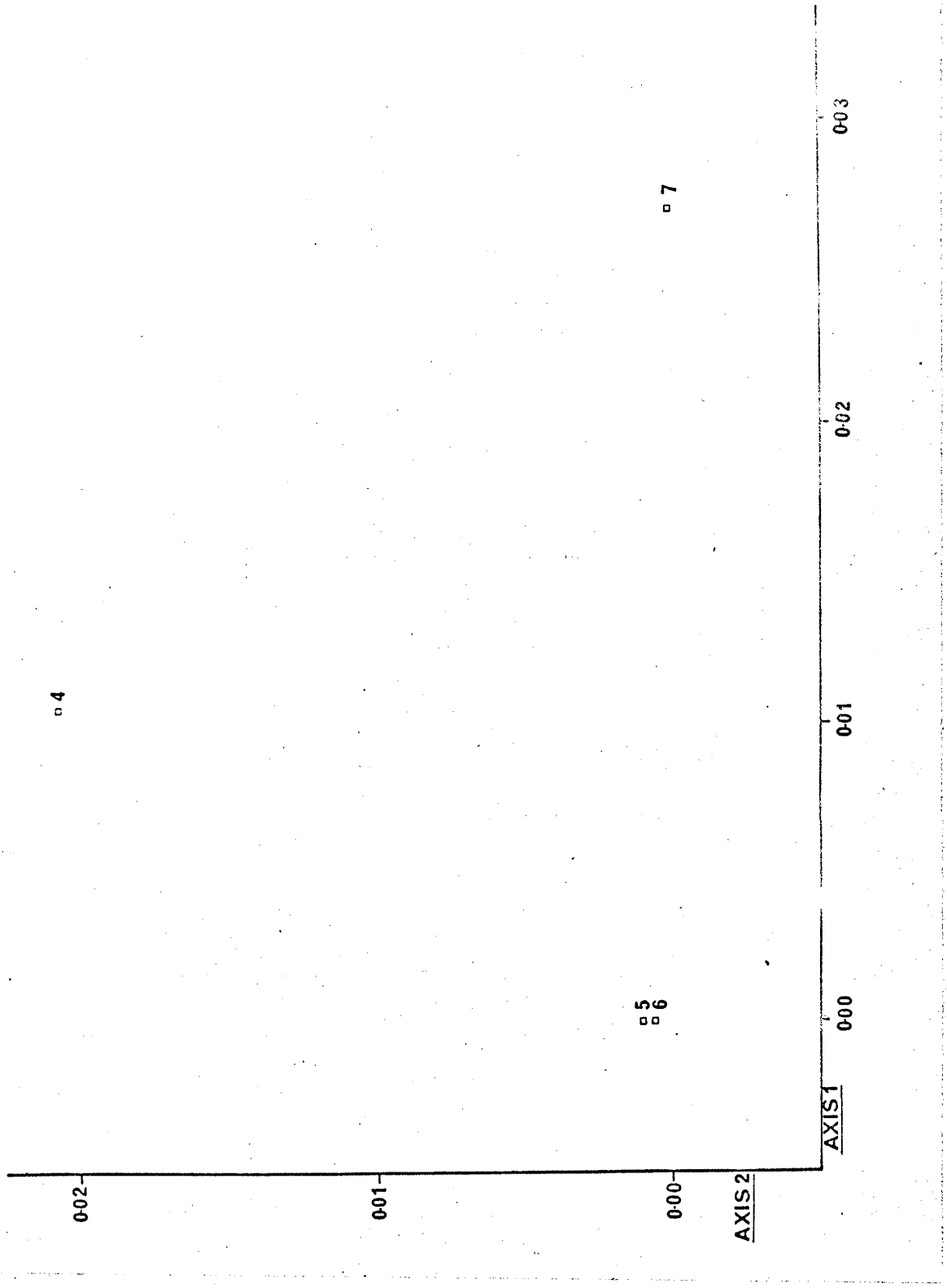

Fig. 8. Pseudotsuga menziesii. Analysis of rate of fall of selected plant nutrient elements for samples 4 to 7. Mean canonical points.

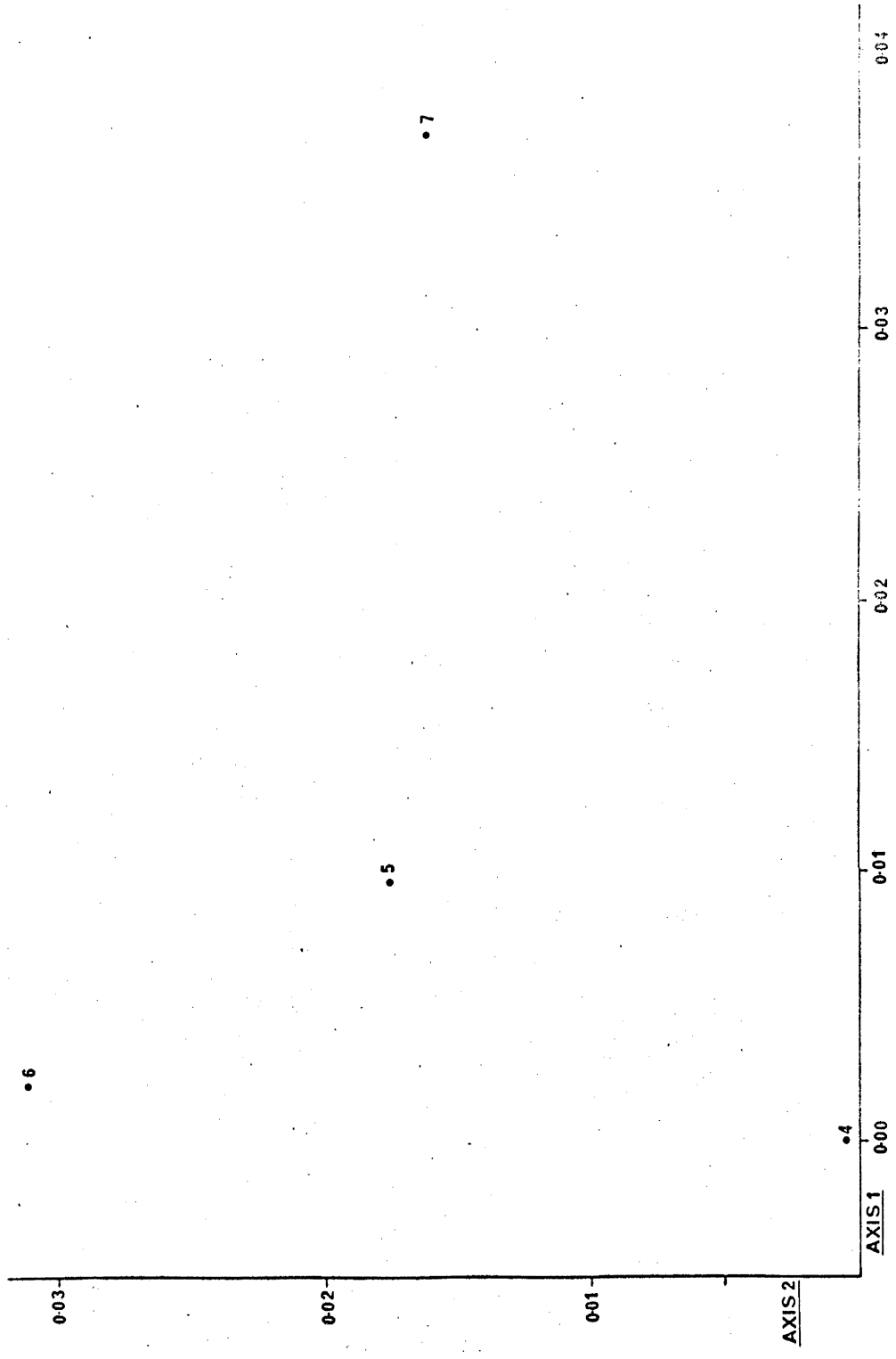

Fig. 9(a). Axes 1 and 2. Pinus nigra var. maritima. Analysis of rate of fall of selected plant nutrient elements for samples 4 to 7. Mean canonical points.

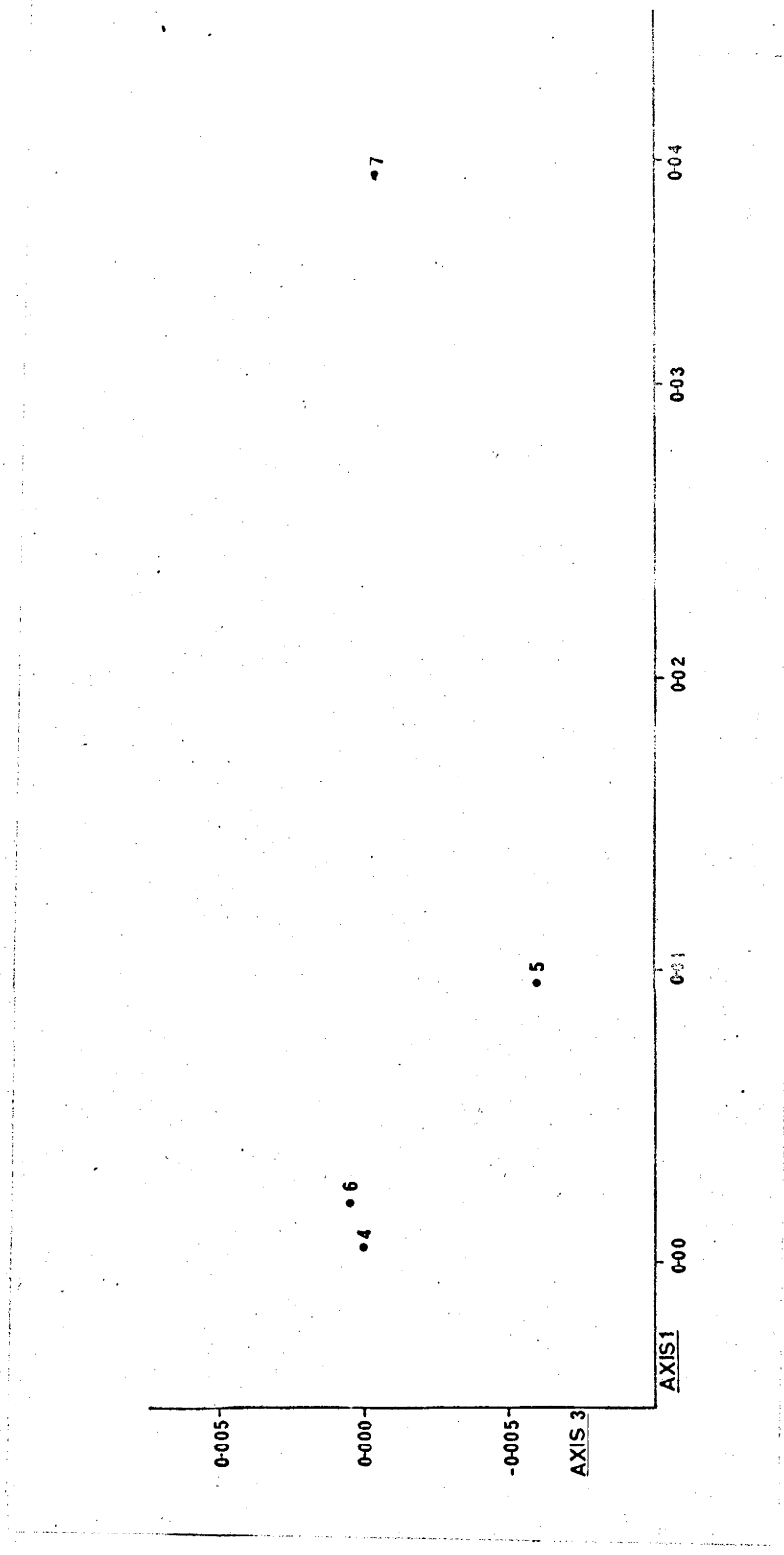

Fig. 9(b). Axes 1 and 3. Pinus nigra var. maritima. Analysis of rate of fall of selected plant nutrient elements for samples 4 to 7. Mean canonical points.

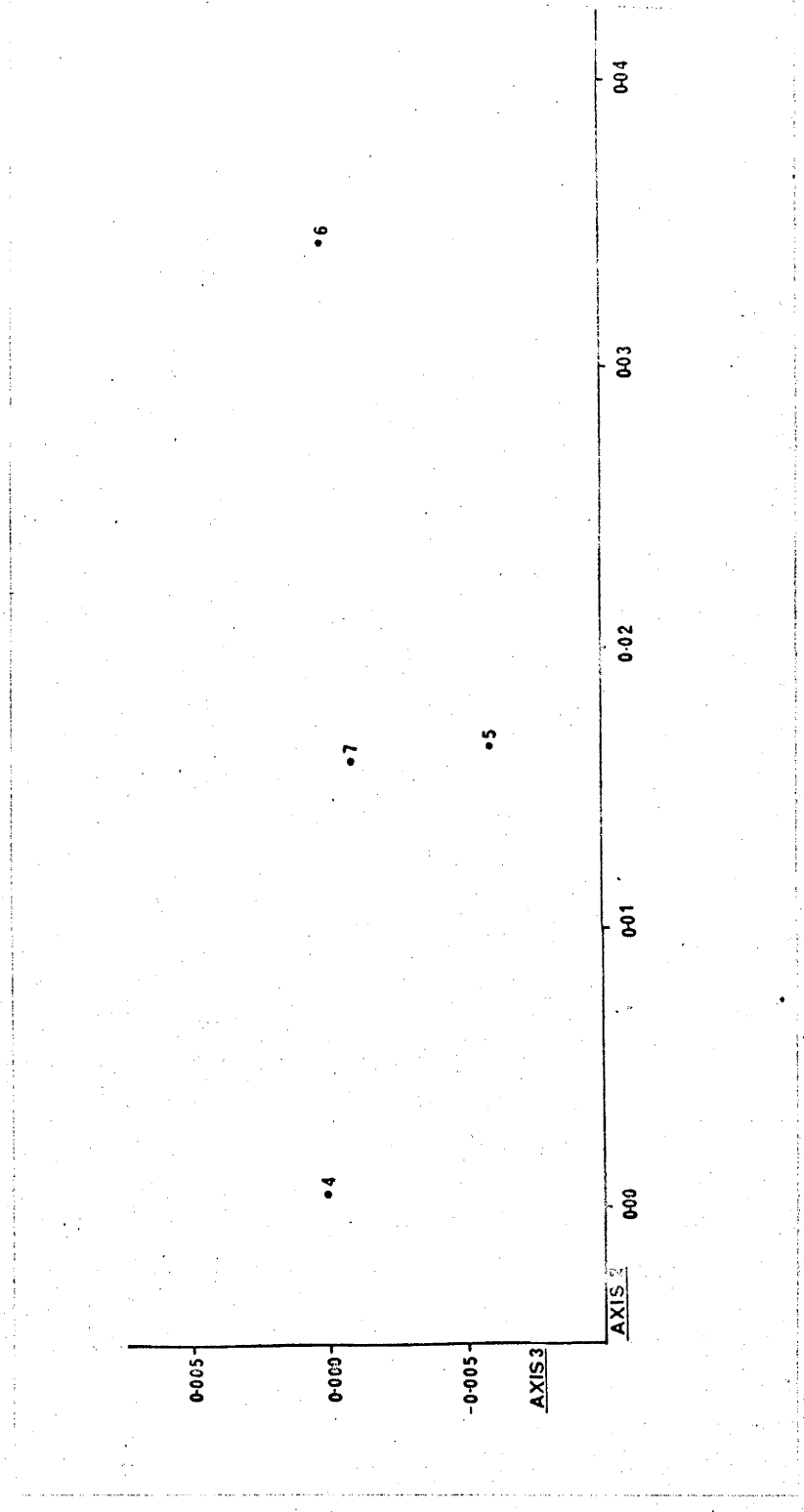

Fig. 9(c). Axes 2 and 3. Pinus nigra var. maritima. Analysis of rate of fall of selected plant nutrient elements for samples 4 to 7. Mean canonical points.

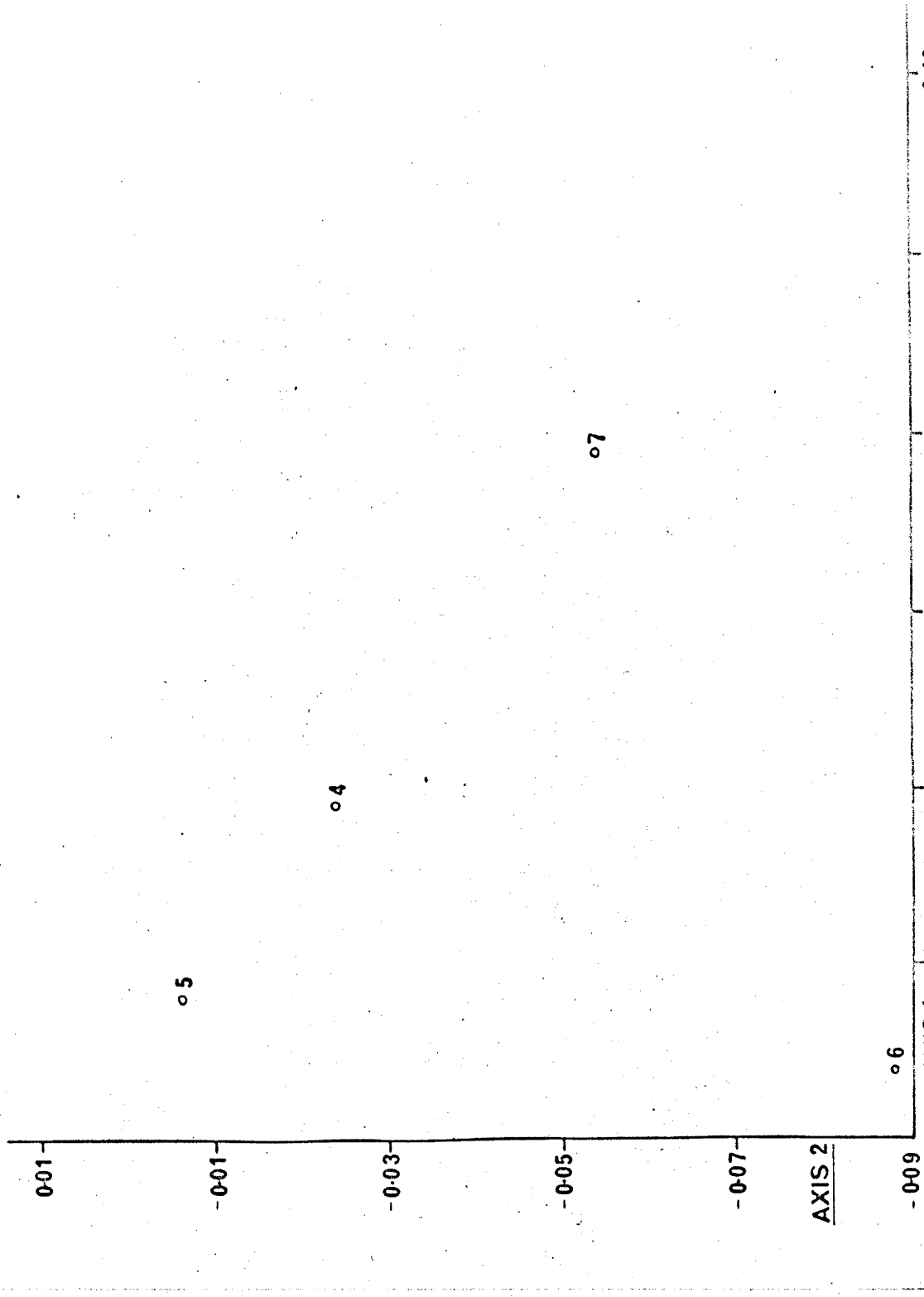

Fig. 10. Pinus ponderosa. Analysis of rate of fall of selected plant nutrient elements for samples 4 to 7. Mean canonical points.

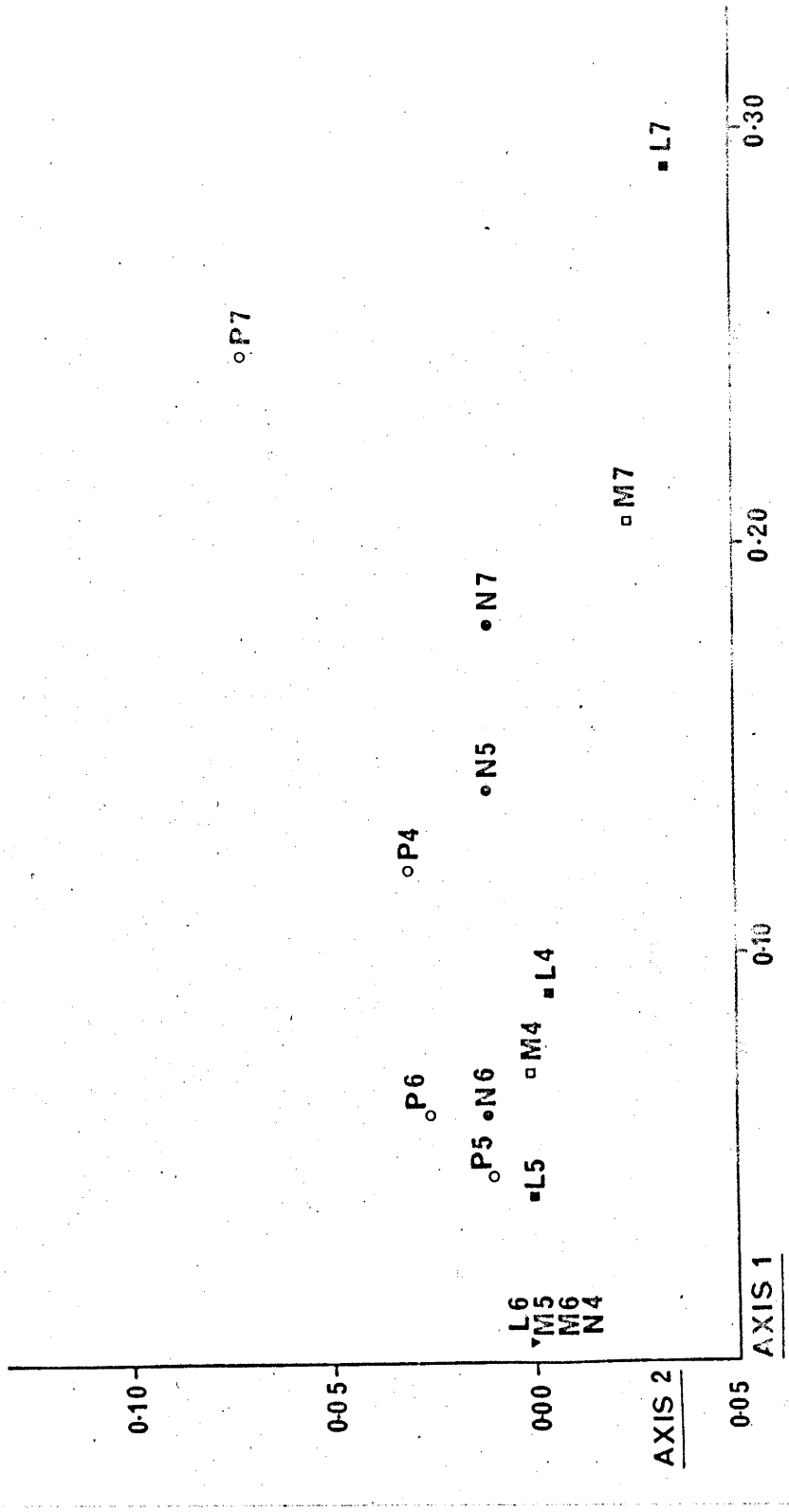

Fig. 11. Combined analysis of rate of fall of selected plant nutrient elements. Mean canonical points.

CHAPTER FOUR

A PRELIMINARY STUDY OF THE SPATIAL DISPOSITION OF CONIFER LITTERFALL ACCESSION; ITS PHYSICAL COMPONENTS AND SELECTED OF ITS PLANT NUTRIENT ELEMENTS

INTRODUCTION

Many studies of forest soils, either chemical or biological in nature, have approached sampling with an implicit assumption of randomness in the spatial distribution patterns of chemical elements and other factors of the soil and litter material. The studies of Zinke (1962) revealed a non random spatial pattern in the distribution of nitrogen and other selected soil properties under individuals of several tree species.

The causation of the observed pattern is of some interest. The influences are undoubtedly multiple but a useful initial model would be to regard the character of a forest soil at any point as the sum of the influences of litterfall, leachates, rainfall and dust accessions. Around the roots, rhizosphere exudates may also contribute significantly (Rovira, 1969).

Litterfall is the main accession route for the supply of organic matter and most plant nutrient elements to the forest floor and it is this influence that was chosen for investigation in the present study.

Consequent upon the presence of predictable or

known variation in accession patterns of the various physical fractions of litterfall is the likelihood that either or both the concentrations of chemical elements and their total weights accessed per unit area may also be subject to spatial variation.

Two factors, the sizes of the trees surrounding any sampling point and a distance effect, might control accession patterns. The effect of distance from trees would be reflected in the individual accession patterns of the physical fractions of litterfall.

Confirmation of these relationships would raise considerable and important implications for sampling many chemical and biological attributes of forest soils. Stratified sampling plans could be developed which might lead to an increased accuracy and repeatability of assessment.

An experiment was designed to assess these relationships in the four stands used for the previous study. More than one species was used since it was considered that this would greatly enhance the generality of any effects demonstrated. Also of interest is the contrast between accession patterns of the more conical photosynthetic envelope of the three Pinus species and the somewhat umbrella shaped crown of Pseudotsuga menziesii.

METHODS

The methods used for sampling litterfall are described in Chapter Three.

RESULTS

Sample data, for all species at each collection, on the weights of the physical components of litterfall, its plant nutrient chemical concentrations and the weights of chemicals assessed are presented in Chapter Three.

Regression Parameters

Independent variables measured were the diameters at 130cm. over bark (dbh) of the nearest four trees to each litterfall trap and the distances of the sampling points from the nearest parts of the trunks of these same four trees. The independent variables are designated by letters and numbers indicating their natures. Thus, DI is the vector of distances from the sample points to the nearest trees and SI the sizes of these same trees.

The dbh measurements were considered as predictors of canopy weight. Tree diameters undoubtedly altered during the course of the study but this parameter was intended to serve as an index of differential canopy size rather than an absolute measure.

The distance measurements were considered as predictors for Tree I, of variation in canopy density above the sampling points. No previous information on the nature of this relationship appears to be available from the literature.

Table 16 presents means and ranges for the independent

variables.

STATISTICAL ANALYSIS

In the analyses that follow all weight data were analysed as their natural logarithms and concentrations as angles (inverse sine transformation).

Pattern of Leaf and Wood Accession

An initial multiple regression model of the following form was set up:

$$y = b_o + b_1x_1 + b_2x_1^2 + b_3x_2 + b_4x_2^2 + \ldots$$
$$\ldots + b_{16}x_8^2 + e \qquad \ldots\ldots(1).$$

Another of the form:

$$y = b_o + b_1 \sum_{i=1,4} D_i + b_2 \sum_{i=1,4} D_i^2 + b_3 \sum_{i=1,4} S_i + \sum_{i=1,4} S_i^2 + e \qquad \ldots\ldots(2).$$

was also tested. This latter model implies that the coefficients for distance and size relationships are similar and thus the effects for each group of variables may be summed. However, testing of this model showed that it explained consistently less of the total variance than did (1) and was rejected.

Multiple Regression Analysis

Weights of both leafy and woody components of litterfall collected at each sampling occasion were regressed against the independent variables, and their squares,

using a stepwise multiple regression procedure.

Results of these regression analysis are presented in Tables 17 and 18 for leaf and wood respectively. F levels and the coefficients of determination are listed for each regression where all partial regression coefficients were significantly greater than zero ($P<0.05$). The partial regression coefficients and their individual significance levels are presented in Tables 19 and 20.

Coefficients

The nature of the relationships shown by the multiple regression analyses demonstrates that there is, as expected, a considerable difference between the accession patterns of woody and leafy litterfall fraction wherever some relationship was able to be established.

Leaf Material.

In all of the analyses the size coefficients appeared more regularly than those of distance. Most frequently, the coefficients of size of trees I and II were predominant with those of III and IV appearing occasionally. All size coefficients were positive indicating, not unexpectedly, a larger fall around trees of increasing size.

The negative distance coefficients indicated in all cases a decreasing accession with increasing distance from Trees I and III. The reason for inclusion of D_3 is unclear. However, because of the nature of the stepwise procedure this variable may have been included due to its correlation with others (Cassie and Michael, 1969; Snedecor and

Cochran, 1967).

Woody Material.

With this fraction, the distance coefficients tended to appear more often than those of size and more variables to contribute to the relationships.

Where distance coefficients contributed significantly ($P<0.05$) to the regressions DI was usually the most important. In P. lambertiana the coefficient for DI was positive and quadratic possibly indicating a maximum fall away from the trunk. Overall distance relationships with Tree I were generally negative indicating a higher fall close to the tree.

Size factors appear unimportant in P. lambertiana and possibly also in Ps. menziesii. In P. ponderosa however, the size coefficients contribute to the regression, and particularly the direct effect of the size of Tree I emerges as important.

It would seem that the accession patterns of the physical fractions of litterfall in forests are in part 'explained' by linear combinations of variables comprising measures of the size of trees surrounding any sampling point and the distances of these trees from the latter. Moreover, leafy and woody material seem to differ in their accession patterns. Whereas the size effect is more important for the leaf fraction, distance is more important for woody material, which is composed of twigs and, close to the tree, bark in those species that readily shed it. This is reflected in the negative coefficients for DI for all species except P. lambertiana where the woody component

comprised mainly twigs and the corresponding DI coefficients were positive.

Pattern of Element Accession at Each Sample Interval

It is of considerable interest to discover whether the fall of elements or their concentrations over a sampling interval display any definable patterns with relation to the size/distance parameters described above.

A convenient preliminary way of testing the null hypothesis that there is no relationship between the concentrations or weights of plant nutrient elements accessed over any sampling period and the size/distance parameters is through the use of canonical correlation analysis.

The present analyses were set up with eight left hand variables (predictors) representing respectively the distances to and the d.b.h. of tree I to IV from the sampling points. The right hand variables (criteria) were, in the first analysis the weights of eight plant nutrient elements accessed over the sample interval in question and in the second, their concentrations. All computations were performed on data that had been centred by variable means to permit a readier interpretation of the coefficients.

The concentration and rate of fall data for all species and all sample intervals were subjected to the canonical correlation analysis described above. Results of these analyses are expressed in Tables 21 and 23 and the

coefficients for each significant ($P<0.05$) canonical correlation are presented in Tables 22 and 24.

Accession Pattern in the Concentrations of Selected Elements

Relationships were demonstrated between the predictors and criteria over at least one collection for each species. The association between the two sets proved strongest in Ps. menziesii and P. lambertiana where more than half of the collection interval analyses were found to be significant ($P<0.05$). In P. nigra and P. ponderosa the association proved significant at only one collection interval. Where the analyses were found significant, there appeared to be an association with the time of highest nutrient status except for P. nigra (Chapter three). There was little association with the fall of organic matter over sample intervals within species.

Evaluation of coefficients derived from canonical correlation analysis is difficult (P.A.P. Moran, pers. comm.). However, when data are analysed in standardised units those with the greatest absolute magnitudes may be considered the most influential in any association studied. They also suffer from the same drawbacks as multiple regression coefficients in that correlations between variables may cause certain to be given undue weight.

Of the coefficients, those of distance were represented most commonly in the significant ($P<0.05$) associations. DI was negative in the three Pinus species

wherever it was present while in the Ps. menziesii analyses the DI coefficients were both positive and negative at different sample intervals.

Size coefficients were predominantly negative for tree I. Little pattern can otherwise be discerned.

Accession Pattern in the Fall of Selected Elements

Significant associations between the predictors and the criteria proved more common and were generally at a higher level of significance than in the concentration analyses. At least half of the collections for each species proved to have a significant association with the predictors although in no species were all so.

No constant relationship between significant associations of predictors and criteria and the order of totals or level of litterfall could be discerned. In P. nigra and P. lambertiana though, significant associations occurred at the times of least accession of the physical components of litterfall and certain of its constituent mineral elements.

The size and distance coefficients were approximately equally represented among those of greater magnitude. Of these, the DI coefficients were negative in most cases and the SI positive.

DISCUSSION AND CONCLUSIONS

From the results presented above, it may be concluded that the accession of both physical and chemical components of litterfall from conifers varies with a linear combination of the distances to and sizes of the surrounding trees. The relationships are mostly non-linear and the resolution of the pattern of effects further complicated by the presence of correlations between the independent variables. The relationship of litterfall at any point with the diameter of the bole of the tree from which the litterfall is being collected is probably exponential. This is suggested by the known exponential relationship between canopy weight and d.b.h. (Kittredge, 1944; Satoo, 1962) and annual litterfall at any point may be considered to be some simple function of canopy weight. Approximation of the former relationships by using linear functions of the independent variables are likely to introduce errors in estimation as well as leading to conceptual problems. It is suspected that ease of fitting may be an overriding factor where linear models are fitted to exponential and other complex data. The precise natures of the distance relationships remains unknown.

Of the physical fractions, leafy material generally has higher coefficients of determination than woody, except in P. ponderosa. Accession of woody material appears to be more positively associated with the base of the tree in the looser barked species such as P. nigra and P. ponderosa but negatively so for P. lambertiana. Leaf

accession appears to be more positively associated with tree size than is the case for woody material. Thus, the accession pattern of litterfall organic matter and its contained chemicals will tend to be species specific and this specificity will probably be reinforced by uniqueness in the accession patterns of other inputs to the forest floor. Generally, accession patterns may be considered as a function of the horizontal distribution of the canopy and the litter falling at any point a simple function of the weight of the component in the canopy directly above.

The variation in concentration of elements in litterfall with the tree size/distance parameters is somewhat weaker than demonstrated for physical fractions but some relationship can be discerned in all species although not over all collection intervals. The negative effects of the distance parameters appear to be more important in this case than those of size. Where size is involved, it usually has a negative effect as would perhaps be expected from the work of Madgwick and Ovington (1959) and Shibamoto and Tajima (1961) who demonstrated that chemical concentrations of selected elements in the leaves and branches were negatively correlated with tree size, as measured by bole girth.

Weights of elements accessed over the sampling period showed a relationship with the size/distance parameters of greater magnitude than for concentrations. All species had significant relationships for at least half of the collection intervals. The coefficients for distance to and size of tree I were most commonly represented being,

respectively, negative and positive. This suggests that accession of the elements determined may be greatest close to the tree and show a general increase with its size.

(a) Distances

Species	Tree I	Tree II	Tree III	Tree IV
P. lambertiana	1.175(0.073-3.057)	2.481(1.435-4.293)	3.163(1.610-5.728)	3.911(2.261-6.321)
P. nigra	0.693(0.038-1.800)	1.770(1.130-2.413)	2.308(1.543-3.073)	2.965(2.438-4.188)
P. ponderosa	0.869(0.032-1.965)	1.965(1.003-3.204)	2.765(1.724-4.350)	3.268(2.442-4.508)
Ps. menziesii	0.909(0.013-2.273)	1.751(0.505-3.810)	2.291(0.971-4.242)	2.748(1.670-5.372)

(b) Diameters

P. lambertiana	0.382(0.232-0.555)	0.406(0.155-0.595)	0.397(0.132-0.590)	0.388(0.068-0.601)
P. nigra	0.227(0.129-0.441)	0.283(0.115-0.396)	0.265(0.182-0.376)	0.292(0.206-0.354)
P. ponderosa	0.332(0.059-0.508)	0.324(0.117-0.471)	0.316(0.113-0.471)	0.334(0.117-0.473)
Ps. menziesii	0.261(0.089-0.471)	0.282(0.146-0.474)	0.271(0.143-0.410)	0.255(0.094-0.426)

Table 16. Litterfall pattern analysis. Means and ranges for independent variables (metres).

TABLE 17. Spatial patterns in fall of leaf litter. Significant ($P < 0.05$) regression of litterfall on size/distance parameters.

Sample	F level	NDF	P	R^2
L1	7.476	1,38	<0.01	16.44
L2	5.085	3,36	<0.01	29.765
L3	8.172	3,36	<0.01	40.512
L4	6.146	4,35	<0.01	42.305
M1	6.777	3,36	<0.01	36.093
M2	7.493	2,37	<0.01	28.827
M3	5.529	4,35	<0.01	38.720
M4	9.264	2,37	<0.01	33.366
N1	8.526	2,37	<0.01	31.548
N2	15.651	1,38	<0.01	29.171
N3	9.912	3,36	<0.01	45.235
N4	5.892	4,35	<0.01	40.239
P1			n.s.	
P2			n.s.	
P3	5.477	5,34	<0.01	44.611
P4	7.738	2,37	<0.01	29.492

TABLE 18. Spatial pattern in fall of woody litter. Significant ($P < 0.05$) regressions of litterfall on size/distance parameters.

Sample	F level	NDF	P	R^2
L1	4.302	1,38	<0.05	10.169
L2	4.153	1,38	<0.05	9.852
L3	6.379	1,38	<0.05	14.375
L4	5.294	1,38	<0.05	12.228
M1	n.s.		n.s.	
M2	5.320	2,37	<0.01	22.333
M3	n.s.		n.s.	
M4	4.846	2,37	<0.05	20.757
N1	11.605	1,38	<0.01	23.395
N2	12.764	2,37	<0.01	40.826
N3	6.599	2,37	<0.01	26.291
N4	4.876	1,38	<0.05	11.372
P1	9.449	1,38	<0.01	19.91
P2	17.666	2,37	<0.01	48.85
P3	11.890	4,35	<0.01	57.606
P4	6.987	5,34	<0.01	50.679

Sample	Intercept	Coefficient	P	Coefficient	P	Coefficient	P	Coefficient	P	Coefficient	P
L1	0.0289	$0.0614S_2^2$	0.01								
L2	0.0079	$-0.0040D_1$	0.05	$0.0277S_1$	0.05	$0.0295S_2$	0.01				
L3	0.0439	$-0.0042D_1$	0.05	$0.0249S_2$	0.05	$-0.0044D_4$	0.005				
L4	0.2489	$0.1594S_2$	0.025	$-0.0326D_3$	0.001	$0.2104S_3$	0.025	$0.2814S_1^2$	0.01		
M1	0.0109	$0.0228S_2$	0.05	$-0.0014D_1^2$	0.05	$0.0593S_1^2$	0.01				
M2	0.0218	$0.0185S_1$	0.025	$-0.0017D_1^2$	0.005						
M3	0.0364	$0.4080S_1$	0.025	$0.0146D_4$	0.025	$-0.6343S_1^2$	0.05	$-0.0051D_2^2$	0.005		
M4	0.1321	$0.1419S_1$	0.001	$-0.0055D_1^2$	0.05						
N1	0.0869	$0.1292S_2$	0.025	$-0.0102D_2^2$	0.005						
N2	0.0574	$0.3047S_1^2$	0.001								
N3	-0.0014	$-0.0121D_1$	0.05	$0.2630S_1^2$	0.001	$0.2784S_4^2$	0.01				
N4	0.1033	$0.2047S_1$	0.01	$0.2098S_2$	0.05	$-0.0085D_3^2$	0.005	$0.4021S_3^2$	0.05		
P1	n.s.										
P2	n.s.										
P3	0.1291	$-0.0134D_1$	0.01	$0.0675S_1$	0.005	$-0.0714D_3$	0.025	$0.0108D_3^2$	0.025	$0.1502S_4^2$	0.001
P4	0.0892	$0.4174S_1$	0.005	$0.6509S_2^2$	0.025						

Table 19. Spatial pattern in the fall of leaf litter. Coefficients for each significant leaf litterfall regression equation. Probabilities are all less than indicated.

Sample	Intercept	Coefficient	P	Coefficient	P	Coefficient	P	Coefficient	P	Coefficient	P
L1	0.0036	$0.0163D_1^2$	0.05								
L2	0.0098	$0.0090D_1^2$	0.05								
L3	0.0035	$0.0020D_3^2$	0.025								
L4	-0.0092	$0.0024D_2^2$	0.05								
M1	n.s.										
M2	0.0078	$-0.0035D_1^2$	0.01	$0.1073S_4^2$	0.025						
M3	n.s.										
M4	0.0087	$-0.1316S_1^2$	0.025	$0.1838S_4^2$	0.025						
N1	0.0049	$-0.0022D_1$	0.005								
N2	0.0459	$-0.0117D_1$	0.001	$-0.0712S_4$	0.025						
N3	0.0962	$-0.1416D_1$	0.005	$0.0635D_1^2$	0.05						
N4	0.0223	$-0.0083D_1$	0.05								
P1	0.0054	$-0.0035D_1$	0.005								
P2	0.0107	$-0.0123D_1$	0.001	$0.3184S_1$	0.01						
P3	0.1121	$-0.0199D_1$	0.001	$0.0598S_1$	0.025	$-0.5012S_4$	0.025	$0.6882S_4^2$	0.05		
P4	0.1228	$-0.0108D_1$	0.001	$0.0577S_1$	0.001	$0.0405S_2$	0.05	$-0.0729D_4$	0.025	$0.0097D_4^2$	0.05

Table 20. Spatial pattern in the fall of woody litter. Coefficients for each significant woody litterfall regression equation. Probabilities are all less than indicated.

TABLE 21. Canonical correlation analysis of spatial pattern of concentrations of chemical elements in litterfall over each sampling interval. Analyses computed in terms of standardised variables.

Sample	Root	R_c	λ	χ^2	NDF	P
L1	0.6065	0.7788	0.1285	64.6412	64	>0.05
L2	0.7424	0.8616	0.0419	99.9602	64	<0.005
L3	0.6506	0.8066	0.0652	86.0238	64	<0.05
L4	0.5679	0.7536	0.1102	69.4764	64	>0.05
M1	0.4702	0.6857	0.1498	59.7991	64	>0.05
M2	0.6705	0.8188	0.0600	88.6213	64	<0.025
M3	0.6945	0.8333	0.0558	90.9212	64	<0.025
M4	0.6420	0.8013	0.0632	86.9626	64	<0.05
N1	0.6390	0.7993	0.0631	87.0496	64	<0.05
N2	0.5808	0.7621	0.0806	79.3409	64	>0.05
N3	0.6665	0.8164	0.0862	77.2170	64	>0.05
N4	0.4286	0.6546	0.1451	60.8031	64	>0.05
P1	0.6332	0.7954	0.0951	74.1104	64	>0.05
P2	0.6043	0.7773	0.0725	82.6459	64	>0.05
P3	0.7208	0.8490	0.0520	93.1467	64	<0.025
P4	0.6353	0.7971	0.0854	77.5110	64	>0.05

Sample	Roots Removed	Variable Set	LHV distance I		dbh I distance II		dbh II distance III		dbh III distance IV		dbh IV
			RHV	N	P	K	Ca	Mg	Mn	Fe	Zn
L2	0	LHV		-0.0861	-0.2615	0.1470	-0.2268	0.4044	0.0142	0.0484	0.0411
		RHV		-0.3438	0.5881	-0.3405	-0.5655	0.1132	0.0031	-0.2057	0.1956
L3	0	LHV		-0.7057	0.1638	-0.3966	-0.3519	0.2627	-0.4666	0.5807	-0.2908
		RHV		0.0577	0.0131	0.0070	0.0143	-0.2607	-0.4289	0.6370	0.5819
M2	0	LHV		0.7019	0.2348	-0.2319	0.0192	-0.8670	0.0501	0.2249	-0.1293
		RHV		0.9162	0.0580	-0.2129	-0.2764	0.0122	-0.0281	-0.0259	-0.1842
M3	0	LHV		-0.3238	-0.1507	0.2998	0.2382	-0.0094	0.3474	0.7696	-0.0674
		RHV		-0.1421	-0.7810	0.0635	0.4339	0.2905	-0.0907	0.0543	0.2864
M4	0	LHV		0.7746	0.6677	-0.4053	0.1963	0.3576	0.0623	-1.0463	-0.3479
		RHV		0.7811	0.2555	-0.3516	-0.1867	0.2702	-0.2779	0.1045	0.0708
N1	0	LHV		-0.6990	-0.3116	-0.0069	0.5628	0.1879	0.2717	0.0706	-0.1987
		RHV		0.1413	0.5241	-0.3764	-0.0136	0.2225	-0.5654	0.4152	-0.1484
P3	0	LHV		-0.6134	-0.0457	-0.0093	0.2590	0.3393	-0.2496	-0.2752	-0.1606
		RHV		-0.4753	-0.3210	-0.3911	-0.3420	0.0683	0.4936	0.3786	-0.0979

Table 22. Canonical correlation analysis of spatial variation in litterfall element concentration. Coefficients for each significant ($P < 0.05$) canonical correlation.

TABLE 23. Canonical correlation analysis of spatial pattern in weights of elements assessed over each sampling interval. Analyses computed in terms of standardised variables.

Sample	Root	R_c	λ	χ^2	NDF	P
L1	0.5610	0.7490	0.1300	64.2651	64	>0.05
L2	0.6589	0.8117	0.0561	90.7525	64	<0.025
L3	0.7681	0.8764	0.0263	114.6383	64	<0.005
	0.6666	0.8164	0.1133	68.5980	49	<0.05
L4	0.5559	0.7456	0.0942	74.4261	64	>0.05
M1	0.4477	0.6691	0.1447	60.8823	64	>0.05
M2	0.7337	0.8566	0.0509	93.7762	64	<0.01
M3	0.7334	0.8564	0.0316	108.8727	64	<0.005
	0.6732	0.8205	0.1183	67.2250	49	<0.05
M4	0.72932	0.8540	0.0452	97.5070	64	<0.005
N1	0.6538	0.8086	0.0492	94.8914	64	<0.01
N2	0.7109	0.8432	0.0563	90.6283	64	<0.025
N3	0.7571	0.8701	0.0598	88.7446	64	<0.025
N4	0.5297	0.7278	0.0970	73.4975	64	>0.05
P1	0.6236	0.7897	0.1259	65.2636	64	>0.05
P2	0.6457	0.8036	0.0803	79.4224	64	>0.05
P3	0.6416	0.8010	0.0504	94.1145	64	<0.01
P4	0.6708	0.8190	0.0661	85.5928	64	<0.05

Sample	Roots Removed	Variable Set	LHV distance I dbh I N	P	K	distance II Ca	Mg	dbh II distance III Mn	Fe	dbh III distance IV Zn
L2	0	LHV	0.2398	0.2695	0.0146	0.1853	-0.4636	0.0492	-0.1468	0.0426
		RHV	-0.1294	-0.5549	0.0987	0.6601	-0.1314	0.0964	0.3417	-0.2943
L3	0	LHV	-0.2390	0.2106	-0.1594	0.0319	0.0153	-0.0930	-0.0138	-0.0254
		RHV	0.0548	-0.3874	0.4093	0.3018	-0.5303	-0.0367	0.5497	0.0602
	1	LHV	0.0857	0.0317	0.2221	0.2537	-0.2354	0.0716	-0.2320	0.1247
		RHV	0.5648	-0.5369	0.3644	-0.0197	-0.2951	0.2734	-0.0571	-0.3074
M2	0	LHV	-0.4322	0.4485	-0.3509	0.2987	0.1612	-0.0103	0.0025	-0.0389
		RHV	-0.5578	0.1435	-0.0916	-0.1970	0.6423	0.1557	0.4086	0.1160
M3	0	LHV	-0.0370	1.0323	-0.4634	0.1759	0.3126	0.083	-0.2502	-0.2147
		RHV	0.1778	0.1021	-0.5858	0.0356	0.1856	0.071	0.5975	0.4659
	1	LHV	-0.2697	-0.3658	-0.1929	0.2309	-0.0896	0.2655	0.7662	-0.0486
		RHV	-0.2834	-0.6978	0.1983	0.4246	0.4134	-0.1176	-0.0712	0.1530
M4	0	LHV	-0.3340	-0.6219	0.2681	-0.2881	-0.6487	-0.1894	1.2397	0.4342
		RHV	-0.7134	-0.1786	0.3918	0.1834	0.0268	0.2763	-0.4415	0.0085
N1	0	LHV	-0.3892	0.2266	-0.6674	0.5500	-0.0131	0.3806	0.1333	-0.5162
		RHV	0.3565	0.5955	-0.2109	-0.4414	0.4325	0.0001	0.1675	0.2526
N2	0	LHV	-0.4988	0.8801	-0.1211	-0.2714	-0.1910	-0.1980	-0.0564	-0.4648
		RHV	0.6878	0.2957	-0.0084	-0.4233	0.1580	-0.0772	-0.0483	0.4764
N3	0	LHV	-0.0309	0.2220	0.0108	0.0827	-0.0521	0.0935	-0.0594	0.0783
		RHV	0.0761	0.2927	0.3361	0.0985	-0.8641	0.0801	0.1050	0.1474
P3	0	LHV	-0.4849	0.1240	0.0336	0.0108	-0.0646	-0.1257	-0.0095	-0.0102
		RHV	-0.3762	0.1774	-0.3827	-0.2934	0.3752	0.4833	0.4374	-0.1697
P4	0	LHV	-0.0743	0.1957	0.0220	0.0767	-0.0148	0.1877	-0.1453	0.2014
		RHV	-0.1045	0.5660	-0.2016	0.3377	-0.6634	0.0162	0.1232	0.2420

Table 24. Canonical correlation analysis of spatial pattern in weights of elements accessed at each sampling interval. Coefficients for all significant ($P < 0.05$) correlations.

CHAPTER FIVE

SELECTED CHARACTERISTICS OF THE FOREST FLOOR IN A PLANTATION OF CORSICAN PINE

Ebermayer (1876) was one of the first to demonstrate the importance of litter layers in the continued production of forest crops and the study of litter must now be an integral part of any complete investigation of forest ecosystem nutrient cycles. Litter studies allow considerable insight into the energetics and nutrient cycling of forests and provide information of value in their efficient management.

Large amounts of organic matter accumulate in many mor litters and a considerable proportion of the total supply of plant nutrients within an ecosystem may thus become partly immobilised (Ovington, 1962; Rodin and Bazilevich, 1967) to be only slowly released through leaching and the action of heterotrophic decomposers.

In Australia, as in many other countries, mor forming species are being planted on soils that were developed under grassland or broadleaf forest associations. The litter layers developed as a result of this change in vegetation are qualitatively different from the former giving rise to a more uniform environment with an altered set of biological relationships.

Litter layers may be modified by management practices and the prescribed burning and grazing advocated for

certain forests entail risks of nutrient losses from the forest system through volatilisation, solubilisation and by exposure of the soil to erosion.

The objects of the present study were to assess the magnitude and temporal variation of the pool of organic matter and its contained plant nutrient elements in the litter layers of a corsican pine (Pinus nigra Arnold var. maritima (Aiton)) stand. Results obtained are compared with those obtained in 1968 during a broad survey of the forest floors of several other conifer species growing in the same immediate locality.

METHODS

For the initial survey, samples were taken at random within stands of Pinus banksiana Lambert, Pinus jeffreyi A. Murray, Pinus lambertiana Douglas, Pinus ponderosa Douglas, Pseudotsuga menziesii (Mirbel) (two provenances) and Larix decidua Miller. Twelve cores (10 cm. x 10 cm.) were taken from within each stand in June and November, 1968.

Sampling of the P. nigra stand extended from July, 1969 to October, 1970 (Table 29). Cores were again 10 cm. x 10 cm. and selected randomly from within untreated plots of another experiment (Chapter six) and an adjacent supplementary plot. Data given for litter weights but not for chemical analytical results include figures from plots treated with the pesticides carbaryl and DDT.

In all stands sampled, canopies were closed and the litter layers well developed. With the exception of the

L. decidua stand, ground vegetation was restricted to the occasional presence of Pteridium esculentum (Forst. f.).

The litter cores comprising each sample from the P. nigra stand were returned to the laboratory in individual containers and the mesofauna extracted using modified Tullgren funnels. The cores were then sorted into L and FH layers, dried at 80°C., weighed and ground to pass a 1.3 mm. sieve in preparation for chemical analysis.

All samples were analysed for nitrogen (total), phosphorus (total), potassium, calcium, magnesium, manganese, iron and zinc. Results of iron determinations from the 1968 samples were discarded because of analytical error.

RESULTS

DATA SUMMARIES

1968 Survey

The mean weights of the litter layers in the several conifer stands studied are presented in Table 25. Concentrations of the seven elements determined are presented, for both the L and FH layers, in Tables 26 and 27 for the seven stands studied. Table 28 presents the total weights of these elements in the litter layers.

Pinus nigra Studies

Pinus nigra litter was sampled on seven occasions

over the fifteen month period from July, 1969 to October, 1970. Dates, sampling intensities and the mean weights of the L and FH layers at each sampling period are presented in Table 29. Concentrations of the eight elements determined are presented in Tables 30 and 31. The weights of these elements in both litter layers are presented in Table 32.

STATISTICAL ANALYSIS

LITTER LAYER WEIGHTS

The significances of the differences between samples were assessed using Gabriel's STP for the L, FH and total litter layer weights. Results are presented in Table 33 as non-significant subsets at $P<0.05$.

LITTER ELEMENT CONCENTRATIONS

Both Gabriel's STP and CVA were computed from the data of the five samples taken from November, 1969 to October, 1970 for both the L and FH layers.

Significant roots are presented in Tables 34 and scaled vectors for all useful roots in Table 35. Plots of sample mean canonical points on all useful roots are presented in Figs. 12 and 13 for the analyses of the L and FH layers respectively.

CVA reduced the data for the L and FH layers to two and three useful roots explaining, respectively,

approximately 91 and 98 per cent. of the total variance. For both analyses, mean canonical points were well separated and in the L layer plots no groupings were discernable. In the FH layer plots, the samples of April, July and October, 1970 are grouped separately from those of the previous November and December. Tests of the significance of intersample differences, using Gabriels STP, showed that the samples were all significantly different at $P<0.05$ (Table 36). Analysis of totals showed that in the L layer, concentrations of elements in most samples did not exhibit significant ($P<0.05$) differences in this respect suggesting that those noted are due to variation in contrasts. One exception is the sample of July, 1970 when concentration totals were significantly lower. In the FH layers, three significantly different groupings of samples emerged with the highest totals occurring in early summer and lowest in mid-winter. A third group, intermediate between the two, comprised samples from Autumn and Spring.

Efficient discriminators for the L layer CVA were nitrogen, phosphorous and to a lesser extent, iron. For the FH layers, iron, nitrogen and manganese provided most of the discriminating power.

Univariate STP analyses of the significance of the differences between samples are presented in Tables 37 and 38 for both layers and each of the elements assessed.

LITTER ELEMENT WEIGHTS

Both forms of multivariate analyses were also computed

for the weights of the eight elements assessed for the six samples taken from October, 1969 to October, 1970. Data matrices were generated as the sum of the products of the vectors of litter weights for each layer and the corresponding matrices of elemental concentrations.

Significant roots for the CVA of these data are presented in Table 34. Results were examined on two useful roots explaining approximately 92% of total variance. Sample mean canonical points are plotted in Fig. 14 and show the occurrence of three groups of samples. These are, firstly the samples of October, 1969 and November, 1970; secondly those of December, 1969 and October, 1970 and, finally, those of April and July, 1970. The STP analysis showed that the samples within each of these three groups were not significantly different ($P<0.05$) considering all elements simultaneously. Analysis of totals (Table 40) showed that the differences between samples could not be attributed to variation in totals since the only sample to vary significantly was that taken in mid winter 1970 which exhibited a minimum at this time. The best discriminators proved to be nitrogen, iron and to a lesser extent, potassium (Table 35).

Results of univariate STP analyses for each element are presented in Table 39. These analyses indicate that nitrogen, magnesium, manganese and possibly zinc all exhibit winter minima whereas calcium, potassium and phosphorous show no significant temporal variation.

DISCUSSION AND CONCLUSIONS

TEMPORAL VARIATION IN LITTER CHARACTERISTICS OF P. NIGRA

While total weight of the P. nigra litter layers did not vary significantly with the sampling intensity applied, there still remains the possibility of a change. Indeed, it is unlikely that, at the age of the stand, a true weight equilibrium would have been attained. Litter consisted of varying proportions of L and FH material at different times of the year. This may be due to a relatively rapid breakdown rate initiated in early spring and coinciding with the late spring/summer period of increased litter fall accession. After this the L layer slowly loses weight, by leaching and solubilization of material, to the increasing FH.

With the single exception of calcium, concentrations of all elements were greater in the FH than the L layer. The slight increase in L layer calcium concentrations was associated with a fall in the weight of this layer suggesting that this element is largely retained in an immobile state, possibly within the cell walls (Burges, 1956).

Seasonal variation in the concentrations of certain plant nutrient elements in litter has been recorded for conifers (Usher, 1970) and it appears that, for the L layer at least, this may be largely dependent on the marked seasonal variation of litter fall inputs. Another factor is the input of elements in dust and rainfall which,

in Australia, may be considerable. This complicates resolution of the source of the variation observed in litter. Nevertheless, it is considered that concentration increases in the FH layer of, for example, iron and magnesium may represent aeolian inputs when they are not accompanied by corresponding changes in the L layer.

In spite of the foregoing, certain elements exhibited variation suggestive of cycles. Nitrogen showed a winter minimum in the L layer, as did iron, manganese and magnesium in both layers.

Usher (1970) has suggested that survey work should be carried out during the spring and early autumn since many litter characteristics are close to their annual mean values at this time. In the present study total weight of the forest floor did not vary significantly but mean values are nearest to those of the summer and autumn samples. For the various plant nutrient chemicals assessed, the situation is somewhat variable since certain of them are closest to their annual means at different times in both layers. However, autumn appears to be the best time overall and certainly the most favourable for sampling macronutrient elements.

When weights of the selected nutrients are considered, samples from within the various seasons tend to be most similar. It would be of interest to compare seasonal samples from a longer time period in all cases. The pools of individual elements in the litter layers tend to divide into two groups, those showing little or no variation and those showing more marked change. For the elements

exhibiting winter minima it appears that the period of major accession extends from late spring to autumn and that they undergo a gradual decline until the next period of major accession. The elements showing no significant temporal variation are of interest because of their diverse mobilities. Calcium is largely immobile, potassium is lost very rapidly and phosphorus is somewhat intermediate between the two. For potassium, at least, this may be due to provision of balancing amounts supplied from foliar washings or leachates.

INTERSPECIFIC COMPARISONS

Forest Floor Weights

When compared with the species studied during the 1968 survey, the weight of the forest floor in the Pinus nigra stand is considerable. It is only exceeded by those of P. ponderosa and P. jeffreyi; species with a much larger standing crop biomass in this locality. In other parts of the world P. nigra does not appear to have such a well developed forest floor as shown by the lower figures published in Minderman (1968) and Ovington (1950 and 1954).

Pinus radiata is the most important conifer species grown commercially in temperate Australia and comparison with data from P. nigra stands is of some interest. Will (1966) records an estimate of 56 x 10^3 kg./ha. for the total weight of the litter layers of a high producing P. radiata stand in New Zealand. However, values presented here for

P. nigra are generally in excess of those of Forrest and Ovington (1970) and Tanton (unpublished) for P. radiata growing in the Southern Tablelands area of New South Wales. The former authors further claim that 17 x 10^3 kg./ha. appears to be a maximum for P. radiata in the area. Pseudotsuga menziesii is another commonly grown species in New South Wales and the differing figures presented above for the two provenances demonstrate the variability of this one species within a restricted area. Results presented here lie in the upper range of those for the same species growing in England (Ovington, 1954) but are considerably lower than those for P. nigra. Natural stands of Ps. menziesii in the U.S.A. may have very heavy forest floors, some being as high as 117 x 10^3 kg./ha. (Heilman and Gessel, 1963).

Litter Element Concentrations

Ovington (1954) has stated that Pinus nigra litter tends to be low in nitrogen and ash elements. This is confirmed by the results presented above which are compared with those obtained during the 1968 survey.

Of the species sampled, P. nigra had the lowest phosphorus and magnesium levels in both layers while nitrogen was lowest in the FH layers but second lowest to P. lambertiana in the L layer. Potassium levels in the FH were higher than for the species in the 1968 survey but were intermediate in the L layer. The latter was also true of calcium, manganese and zinc levels in both litter layers.

Litter Element Weights

It is of interest to consider the forest floor as a pool, or reservoir of plant nutrient elements. On this basis, the pools of the elements assessed in the P. nigra stand are compared with those of the species in the 1968 survey.

Nitrogen, phosphorous and calcium levels are in the middle of the range of values for the other species while the pools of potassium and zinc are highest in the P. nigra stand. For the latter element, P. nigra and P. lambertiana have almost identical pool sizes. Magnesium and manganese levels in P. nigra are in the lower part of the range.

TABLE 25. Litter layer weights (kg/m^2) of several conifer stands. Means of samples taken in June and November, 1968.

Species	Layer		
	L	FH	TOTAL
P. banksiana	0.560	1.064	1.624
P. jeffreyi	0.929	2.057	2.986
P. lambertiana	0.927	1.759	2.686
P. ponderosa	1.024	2.015	3.039
Ps. menziesii (i)	0.330	1.090	1.420
Ps. menziesii (ii)	0.523	1.753	2.276
L. decidua	0.299	2.331	2.630

TABLE 26. Concentrations of elements in the L layers of several conifer stands (ppm oven dry wt.). Means of samples taken in June and November, 1968.

Species	N	P	K	Ca	Mg	Mn	Zn
P. banksiana	10665.9	692.1	1202.2	10120.9	492.6	841.4	44.0
P. jeffreyi	9372.6	699.4	1587.7	3393.5	662.1	575.3	37.6
P. lambertiana	5848.6	431.6	964.3	9528.8	754.7	949.3	42.5
P. ponderosa	11946.9	870.6	2193.1	3683.6	742.8	665.6	41.95
Ps. menziesii (i)	13940.0	788.0	1653.6	15545.1	613.7	1367.6	28.1
Ps. menziesii (ii)	12871.7	1020.0	1557.6	13578.3	640.9	2055.3	38.1
L. decidua	16480.6	1358.0	1988.2	7788.5	1155.8	357.1	27.3

TABLE 27. Concentrations of elements in the FH layers of several conifer stands (ppm oven dry wt.). Means of samples taken in June and November, 1968.

Species	N	P	K	Ca	Mg	Mn	Zn
P. banksiana	19188.2	1275.6	1971.9	8091.5	1731.0	1796.0	95.0
P. jeffreyi	18580.4	886.4	1512.9	5022.6	1237.0	725.2	55.0
P. lambertiana	14036.2	857.3	1527.4	8037.5	978.7	1560.0	79.5
P. ponderosa	22002.8	1079.0	1586.9	3967.9	879.8	712.4	51.9
Ps. menziesii (i)	18893.0	1019.5	2096.4	16112.6	1707.6	2098.1	56.7
Ps. menziesii (ii)	19430.9	1247.6	2055.8	14668.1	1730.2	2864.2	37.4
L. decidua	22026.2	2771.7	2206.5	8933.6	2274.1	857.9	57.6

TABLE 28. Weights of elements in the litter layers of several conifer stands (g/m^2). Means of samples taken in June and November, 1968.

Species	N	P	K	Ca	Mg	Mn	Zn
P. banksiana	18.19	1.25	1.90	20.13	1.43	1.64	0.09
P. jeffreyi	41.19	2.22	4.08	11.89	2.89	1.78	0.13
P. lambertiana	25.07	1.57	3.14	20.09	2.06	3.05	0.15
P. ponderosa	48.02	2.67	4.84	10.53	2.23	1.88	0.13
Ps. menziesii (i)	16.76	0.92	1.99	15.19	1.52	1.75	0.05
Ps. menziesii (ii)	29.48	1.94	3.15	23.80	2.39	4.36	0.06
L. decidua	38.02	2.46	3.67	15.44	3.69	1.38	0.10

TABLE 29. Litter layer weights and sampling intensity in a Pinus nigra stand (kg./m^2). Geometric means and 95% confidence limits.

Sample No.	Sampling Date	Sampling Intensity	Litter Fraction		
			L	F+H	total
1	7. vii. 1969	20	0.525 (0.406-0.655)	2.078 (1.705-2.502)	2.632 (2.226-3.089)
2	22. x. 1969	20	0.578 (0.458-0.708)	2.010 (1.846-2.375)	2.704 (2.433-2.997)
3	5 xi. 1969	40	0.871 (0.742-1.010)	1.775 (1.615-1.944)	2.701 (2.528-2.882)
4	28. xii. 1969	57	0.868 (0.740-1.006)	1.927 (1.753-2.112)	2.805 (2.547-3.082)
5	2. iv. 1970	57	0.756 (0.673-0.843)	2.031 (1.902-2.166)	2.809 (2.648-2.977)
6	14. vii. 1970	58	0.752 (0.669-0.838)	2.252 (2.107-2.404)	3.033 (2.863-3.211)
7	28. x. 1970	58	0.348 (0.322-0.376)	2.617 (2.423-2.828)	2.990 (2.791-3.204)
	$\bar{y}$		0.671	2.099	2.811

TABLE 30. Concentrations of selected plant nutrient elements in the L litter layer of a Pinus nigra var. maritima stand. Squared means and 95% confidence limits (ppm oven dry wt.).

Sample	N	P	K	Ca
5. xi. 1969	10083.1 (9372.7-10819.3)	282.5 (224.7-346.9)	1234.1 (1088.9-1388.4)	7667.1 (6880.9-8495.8)
28. xii. 1969	9157.4 (8302.3-10054.4)	465.7 (412.9-521.7)	1226.6 (1067.9-1296.2)	5840.1 (4822.5-6955.1)
2. iv. 1970	5272.3 (4953.2- 5601.4)	488.4 (441.5-537.6)	1542.0 (1384.9-1707.5)	7364.1 (6468.3-8318.1)
14. vii. 1970	5261.1 (5021.4- 5506.5)	432.6 (369.3-500.9)	1067.8 (962.8-1178.3)	6958.8 (6052.9-7927.9)
28. x. 1970	7930.2 (7228.2- 8664.7)	317.9 (251.4-392.2)	993.9 (856.3-1141.9)	8386.3 (8020.2-8760.7)
$\bar{y}$	7540.8	397.4	1212.9	7243.3

TABLE 30. Concentrations of selected plant nutrient elements in the L litter layer of a Pinus nigra var. maritima stand. Squared means and 95% confidence limits (ppm oven dry wt.). (contd.)

Sample	Mg	Mn	Fe	Zn
5. xi. 1969	419.3 (343.5-502.6)	819.6 (761.7- 879.8)	2229.9 (2889.0-2599.1)	37.9 (35.1-40.8)
28. xii. 1969	292.6 (226.9-366.6)	774.5 (674.8- 881.1)	2553.8 (2165.1-2974.6)	43.8 (39.9-47.9)
2. iv. 1970	389.8 (334.5-449.3)	705.3 (623.9- 791.5)	2407.2 (2050.1-2793.0)	40.2 (36.7-43.9)
14. vii. 1970	333.7 (280.7-391.2)	584.6 (442.9- 746.1)	703.0 (536.3- 892.1)	33.9 (31.7-36.2)
28. x. 1970	535.6 (492.4-580.7)	809.9 (624.1-1019.9)	1500.0 (1250.6-1772.0)	42.1 (38.6-45.7)
$\bar{y}$	394.2	738.8	1878.8	39.58

TABLE 31. Concentrations of selected plant nutrient elements in the FH litter layers of a Pinus nigra var. maritima stand. Squared means and 95% confidence limits (ppm oven dry wt.).

Sample	N	P	K	Ca
5. xi. 1969	16638.7 (15610.7-17699.4)	725.1 (670.8-781.5)	2844.0 (2649.4-3045.5)	7408.9 (6640.8-8219.1)
28. xii. 1969	11877.3 (11227.5-12545.3)	746.6 (699.3-795.5)	3265.4 (2912.8-3638.2)	5930.0 (5226.8-6677.5)
2. iv. 1970	11133.7 (10518.9-11766.0)	714.1 (663.3-766.7)	2820.1 (2513.8-3144.1)	6251.9 (5736.4-6789.6)
14. vii. 1970	10849.7 (10334.5-11377.4)	695.3 (650.7-741.4)	2240.4 (2020.5-2471.7)	5939.4 (5266.9-6652.5)
28. x. 1970	10723.0 (10181.4-11278.7)	609.2 (517.6-708.1)	2136.6 (1890.8-2397.5)	5984.6 (5392.5-6607.6)
$\bar{y}$	12244.5	698.1	2661.3	6303.0

TABLE 31. Concentrations of selected plant nutrient elements in the FH litter layers of a Pinus nigra var. maritima stand. Squared means and 95% confidence limits (ppm oven dry wt.). (contd.)

Sample	Mg	Mn	Fe	Zn
5. xi. 1969	790.0 (735.0- 847.0)	1569.4 (1434.3-1710.5)	6669.4 (6140.1-7220.7)	56.6 (53.6-59.7)
28. xii. 1969	932.4 (806.1-1067.7)	1484.7 (1306.4-1674.5)	8866.7 (8024.7-9750.7)	67.1 (60.9-73.7)
2. iv. 1970	499.3 (381.5- 632.9)	975.0 (629.2-1396.4)	3970.0 (3166.3-4864.4)	58.7 (54.1-63.6)
14. vii. 1970	433.5 (367.4- 505.0)	885.5 (595.9-1232.3)	2818.9 (2342.0-3340.0)	46.5 (43.1-49.9)
28. x. 1970	716.4 (606.9- 835.1)	1539.4 (1173.6-1954.8)	5457.9 (4663.5-6314.8)	57.9 (53.7-62.2)
$\bar{y}$	674.0	1290.8	4356.6	57.36

TABLE 32. Weights of selected plant nutrient elements in the litter layers of a Pinus nigra var. maritima stand. Geometric means and 95% confidence limits (g/m^2).

Sample	N	P	K	Ca
28. x. 1969	36.35 (32.85-40.22)	1.73 (1.55-1.94)	6.46 (5.40-7.74)	21.90 (19.03-25.19)
5. xi. 1969	36.79 (32.03-42.26)	1.48 (1.26-1.73)	5.85 (5.06-6.76)	18.48 (15.77-21.67)
28.xii. 1969	31.53 (27.18-36.59)	1.86 (1.61-2.14)	7.30 (6.01-8.87)	16.70 (14.29-19.51)
2. iv. 1970	27.80 (24.62-31.39)	1.92 (1.72-2.14)	7.22 (6.29-8.29)	19.56 (17.33-22.07)
14.vii. 1970	26.23 (24.28-28.33)	1.75 (1.58-1.93)	5.43 (4.97-5.93)	17.67 (15.24-20.50)
28. x. 1970	34.16 (29.38-39.72)	1.87 (1.52-2.29)	6.51 (5.47-7.74)	20.60 (17.17-24.71)
$\bar{y}$	32.14	1.77	6.46	19.15

TABLE 32. Weights of selected plant nutrient elements in the litter layers of a Pinus nigra var. maritima stand. Geometric means and 95% confidence limits (g/m^2). (contd.)

Sample	Mg	Mn	Fe	Zn
28. x. 1969	2.24 (1.92-2.60)	3.86 (3.33-4.47)	15.27 (11.87-19.64)	0.14 (0.12-0.15)
5. xi. 1969	1.69 (1.43-1.99)	3.35 (2.86-3.91)	13.18 (11.29-15.39)	0.13 (0.11-0.15)
28.xii. 1969	2.02 (1.63-2.49)	3.52 (3.00-4.12)	19.08 (15.64-23.28)	0.17 (0.15-0.20)
2. iv. 1970	1.39 (1.09-1.77)	2.54 (1.81-3.55)	10.37 (8.02-13.41)	0.16 (0.14-0.19)
14.vii. 1970	1.13 (0.97-1.32)	2.13 (1.63-2.78)	6.12 (5.23- 7.17)	0.12 (0.11-0.13)
28. x. 1970	2.26 (1.81-2.82)	4.64 (3.39-6.36)	16.19 (12.98-20.19)	0.18 (0.15-0.22)
$\bar{y}$	1.79	3.34	13.37	0.15

TABLE 33. STP analysis of temporal variation in litter weights of a P. nigra stand. Non-significant subsets of samples ($P < 0.05$).

L layer	FH layer	Total
xi. 1969	x. 1970	vii. 1970
xii. 1969	vii. 1970	x. 1970
iv. 1970	x. 1969	iv. 1970
vii. 1970	vii. 1969	xii. 1969
x. 1969	iv. 1970	x. 1969
vii. 1969	xii. 1969	xi. 1969
x. 1970	xi. 1969	vii. 1969

TABLE 34. Canonical variate analysis of temporal variation in the weights and concentrations of selected plant nutrient elements in the litter of a Pinus nigra var. maritima stand. Significant (P <0.05) roots.

Analysis	Order	Eigenvalue	P	% Variance	Cumulative
P. nigra L layer element concentrations	I	7.276	<0.005	65.090	65.090
	II	2.881	<0.005	25.773	90.863
	III	0.558	<0.005	4.992	95.855
	IV	0.463	<0.005	4.145	100.000
P. nigra FH layers element concentrations	I	6.323	<0.005	67.702	67.702
	II	2.164	<0.005	23.172	90.874
	III	0.720	<0.005	7.707	98.581
P. nigra Weights elements in litter layers	I	4.260	<0.005	73.397	73.397
	II	1.101	<0.005	18.966	92.363
	III	0.233	<0.005	4.014	96.377
	IV	0.131	<0.025	2.264	98.641

TABLE 35. Canonical variate analysis of selected litter elements in a *Pinus nigra* var. *maritima* stand. Eigenvectors for all analyses scaled to show the relative discriminating power of each variable.

Analysis	Root	Variables							
		N	P	K	Ca	Mg	Mn	Fe	Zn
L layer	I	12.521	- 8.237	-4.613	1.914	0.461	-3.368	6.401	4.349
(concentrations)	II	2.808	-11.228	-5.975	7.328	19.945	-1.643	-19.969	2.582
FH layer	I	16.392	- 6.711	-4.643	5.551	-2.049	-9.770	19.319	-4.540
(concentrations)	II	-4.363	4.570	-2.792	-1.562	-5.250	-5.309	10.845	5.000
	III	-1.331	- 0.453	-9.069	0.981	5.435	-4.902	4.779	-5.075
Both layers	I	1.655	- 1.006	-1.230	0.424	0.724	-0.748	1.381	-1.132
(element weights)	II	-0.816	0.910	-1.410	-0.407	-0.813	-0.854	2.435	1.357

TABLE 36. STP analysis of selected litter elements in a Pinus nigra var. maritima stand. All variable hypotheses. Non-significant subsets of samples at P <0.05.

Sample Combination	$\theta[0.05]$	θ	P
(a) P. nigra concentrations of selected elements L layer. All subsets significantly different.			
	0.2698	-	>0.05
(b) P. nigra concentrations of selected elements in FH layer. All subsets significantly different.			
	0.2698		>0.05
(c) P. nigra weights of selected elements in total litter			
x. 69, xi. 69	0.2456	0.1814	<0.05
xii. 69, x. 70	0.2456	0.1689	<0.05
iv. 70, vii. 70	0.2456	0.2305	<0.05

TABLE 37. STP analysis of concentrations of selected plant nutrient elements in L layer of a P. nigra stand. Non-significant subsets (P <0.05) of means listed in decreasing order.

N	P	K	Ca
xi. 1969	iv. 1970	iv. 1970	x. 1970
xii. 1969	xii. 1969	xi. 1969	xi. 1969
x. 1970	vii. 1970	xii. 1969	iv. 1970
iv. 1970	x. 1970	vii. 1970	vii. 1970
vii. 1970	xi. 1969	x. 1970	xii. 1969

Mg	Mn	Fe	Zn
x. 1970	xi. 1969	xii. 1969	xii. 1969
xi. 1969	x. 1970	iv. 1970	x. 1970
iv. 1970	xii. 1969	xi. 1969	iv. 1970
vii. 1970	iv. 1970	x. 1970	xi. 1969
xii. 1969	vii. 1970	vii. 1970	vii. 1970

TABLE 38. STP analysis of concentrations of selected plant nutrient elements in the FH layers of a Pinus nigra var. maritima stand. Non-significant subsets of means ($P < 0.05$) listed in decreasing order.

N	P	K	Ca
xi. 1969	xii. 1969	xii. 1969	xi. 1969
xii. 1969	xi. 1969	xi. 1969	iv. 1970
iv. 1970	iv. 1970	iv. 1970	x. 1970
vii. 1970	vii. 1970	vii. 1970	vii. 1970
x. 1970	x. 1970	x. 1970	xii. 1969

Mg	Mn	Fe	Zn
xii. 1969	x. 1970	xii. 1969	xii. 1969
xi. 1969	xi. 1969	xi. 1969	iv. 1970
x. 1970	xii. 1969	x. 1970	x. 1970
iv. 1970	iv. 1970	iv. 1970	xi. 1969
vii. 1970	vii. 1970	vii. 1970	vii. 1970

TABLE 39. STP analysis of temporal variation in the weights of selected plant nutrient elements in Pinus nigra var. maritima litter layers. Non-significant subsets of means listed in decreasing order ($P < 0.05$).

N	P	K	Ca
xi. 1969	iv. 1970	xii. 1969	x. 1969
x. 1959	x. 1970	iv. 1970	x. 1970
x. 1970	xii. 1969	x. 1970	iv. 1970
xii. 1969	vii. 1970	x. 1969	xi. 1969
iv. 1970	x. 1969	xi. 1969	vii. 1970
vii. 1970	xi. 1969	vii. 1970	xii. 1969

Mg	Mn	Fe	Zn
x. 1970	x. 1970	xii. 1969	x. 1970
x. 1969	x. 1969	x. 1970	xii. 1969
xii. 1969	xii. 1969	x. 1969	iv. 1970
xi. 1969	xi. 1969	xi. 1969	x. 1969
iv. 1970	iv. 1970	iv. 1970	xi. 1969
vii. 1970	vii. 1970	vii. 1970	vii. 1970

TABLE 40. STP analyses of temporal variation of totals in Pinus nigra var. maritima litter analyses. Non-significant subsets of samples ($P < 0.05$) in decreasing order of means.

Concentrations of eight elements in L layer

xi. 1969
xii. 1969
x. 1970
iv. 1970
vii. 1970

Concentrations of eight elements in FH layer

xi. 1969
xii. 1969
x. 1970
iv. 1970
vii. 1970

Weights of eight elements on forest floor

x. 1970
xii. 1969
x. 1969
xi. 1969
iv. 1970
vii. 1970

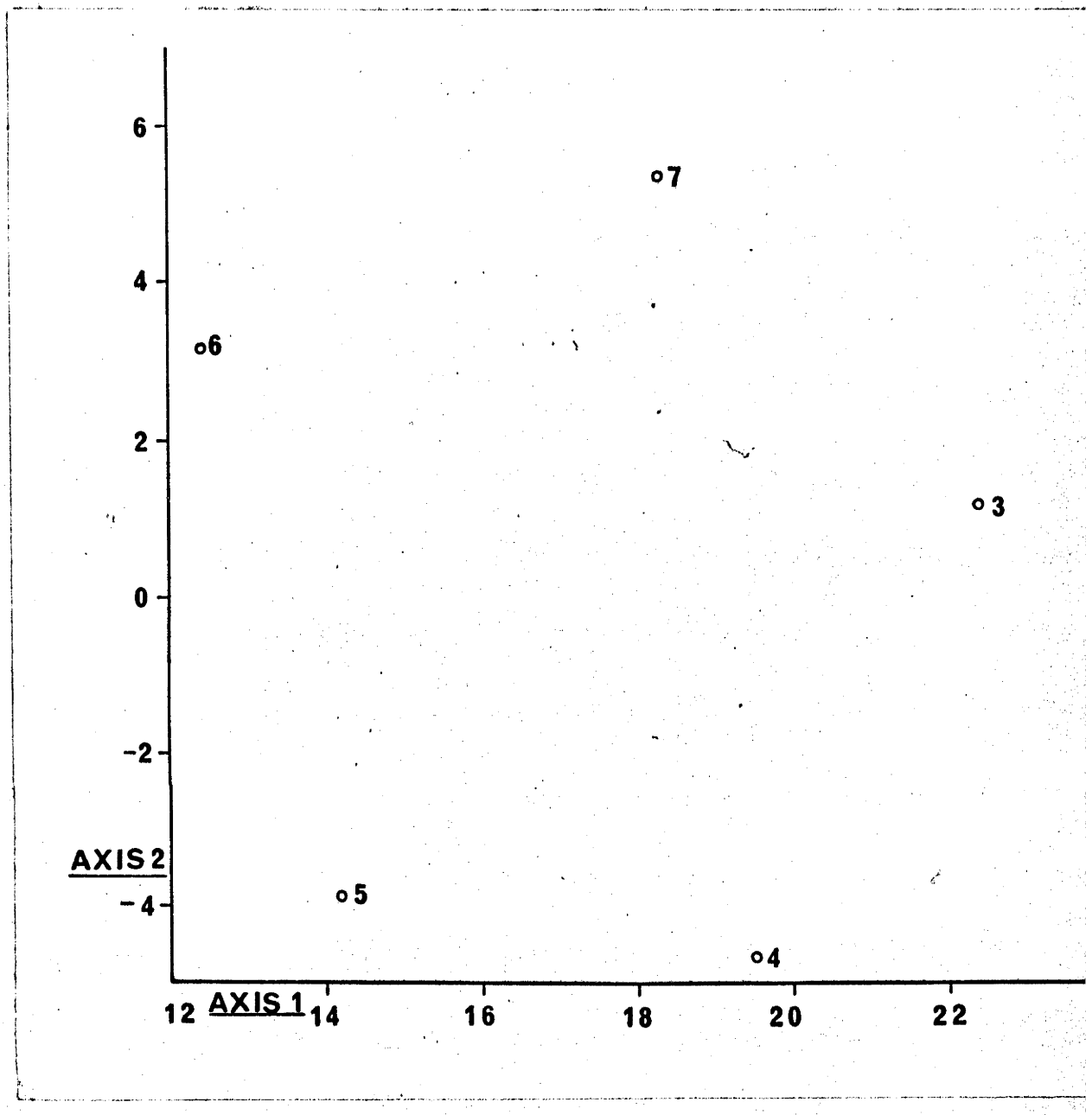

Fig. 12(a). Axes 1 and 2. Pinus nigra var. maritima. Temporal analysis of selected litter chemical concentrations. Mean canonical points of L layer samples.

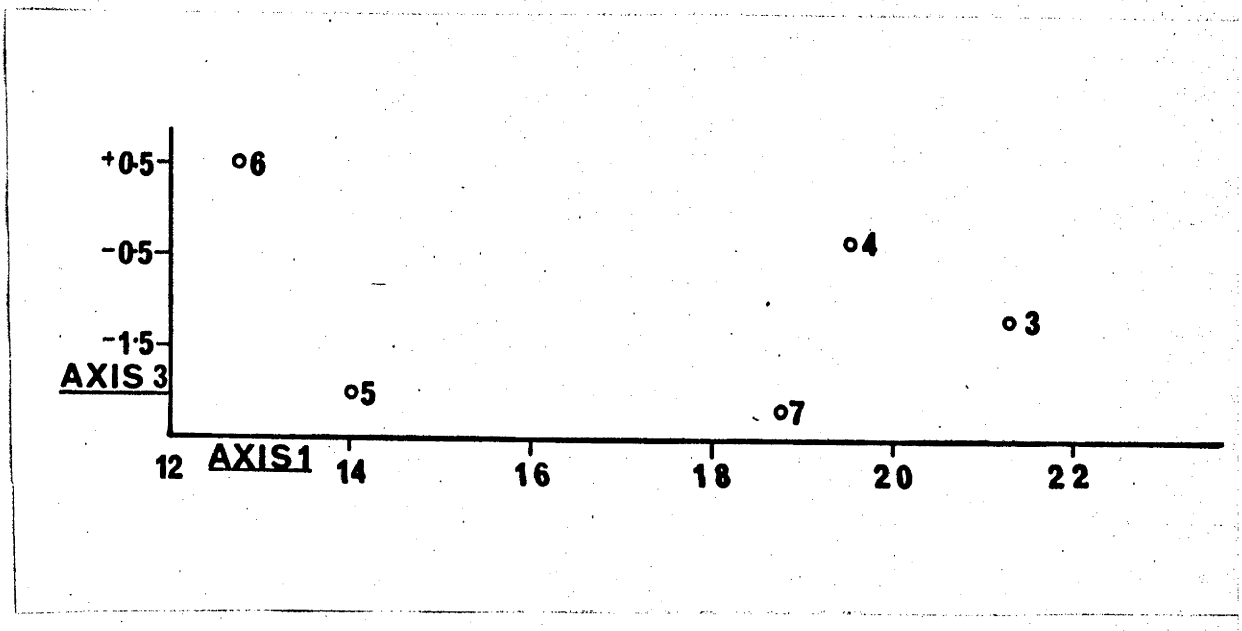

Fig. 12(b). Axes 1 and 3. Pinus nigra var. maritima. Temporal analysis of selected litter chemical concentrations. Mean canonical points of L layer samples.

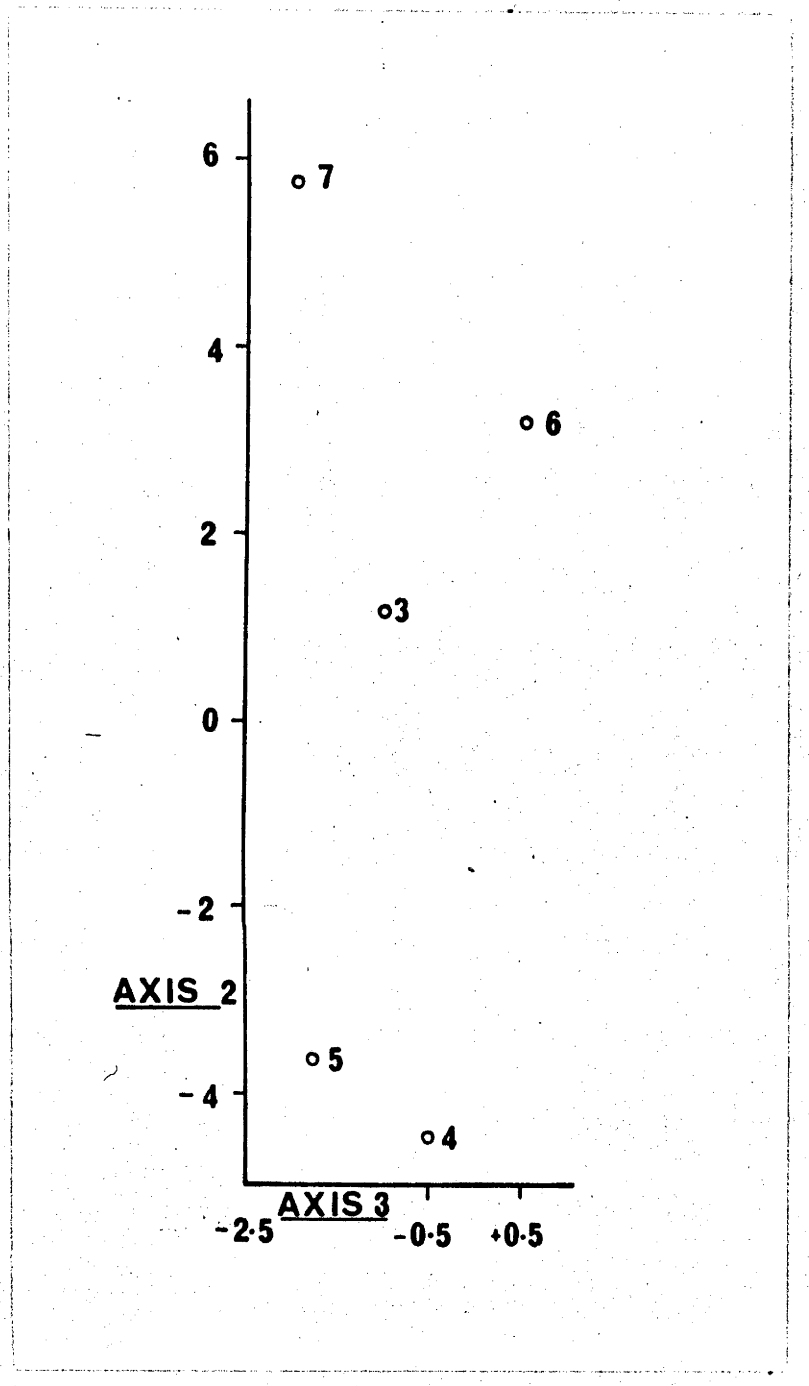

Fig. 12(c). Axes 2 and 3. Pinus nigra var. maritima. Temporal analysis of selected litter chemical concentrations. Mean canonical points of L layer samples.

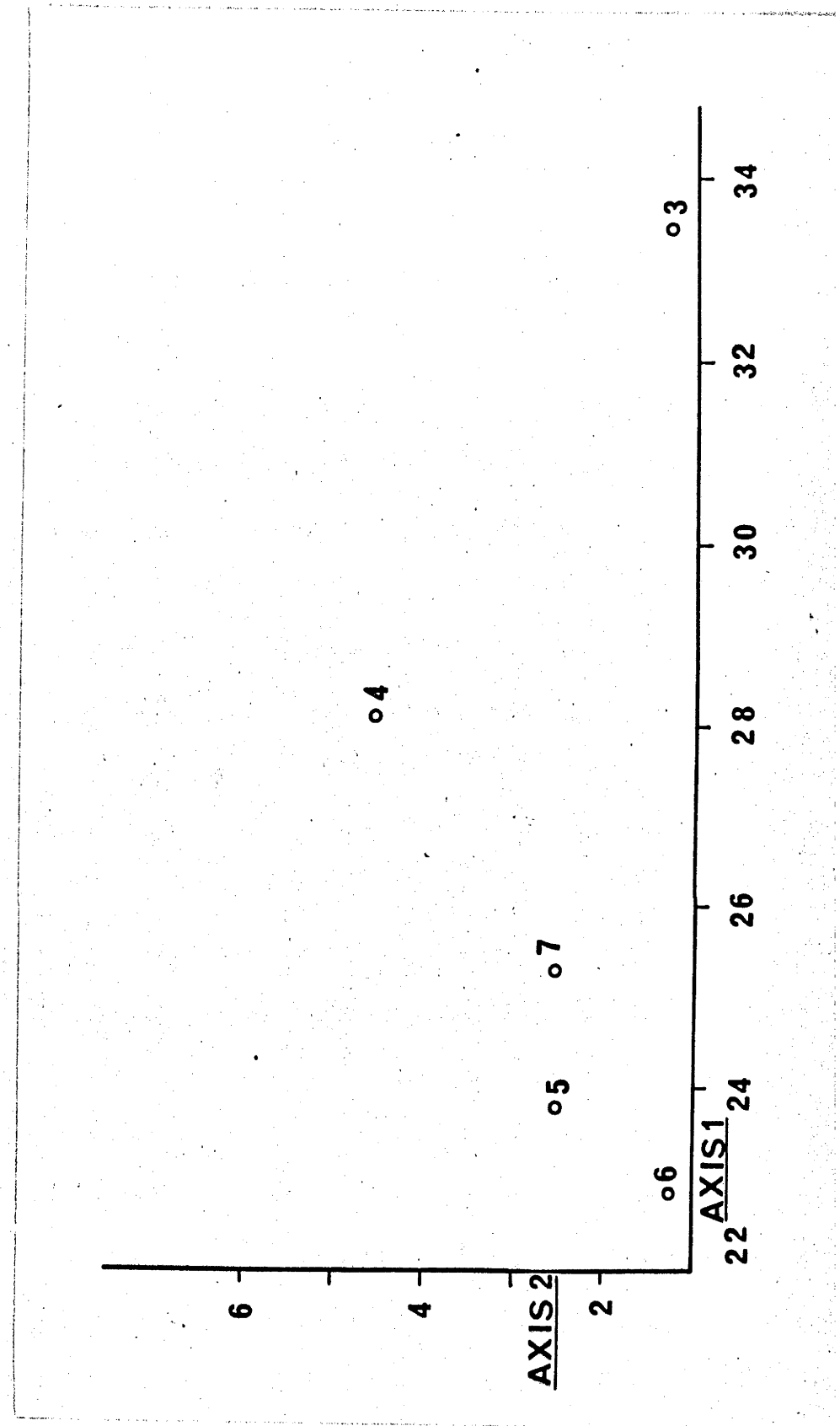

Fig. 13(a). Axes 1 and 2. Pinus nigra var. maritima. Temporal analysis of selected litter chemical concentrations. Mean canonical points of FH layer samples.

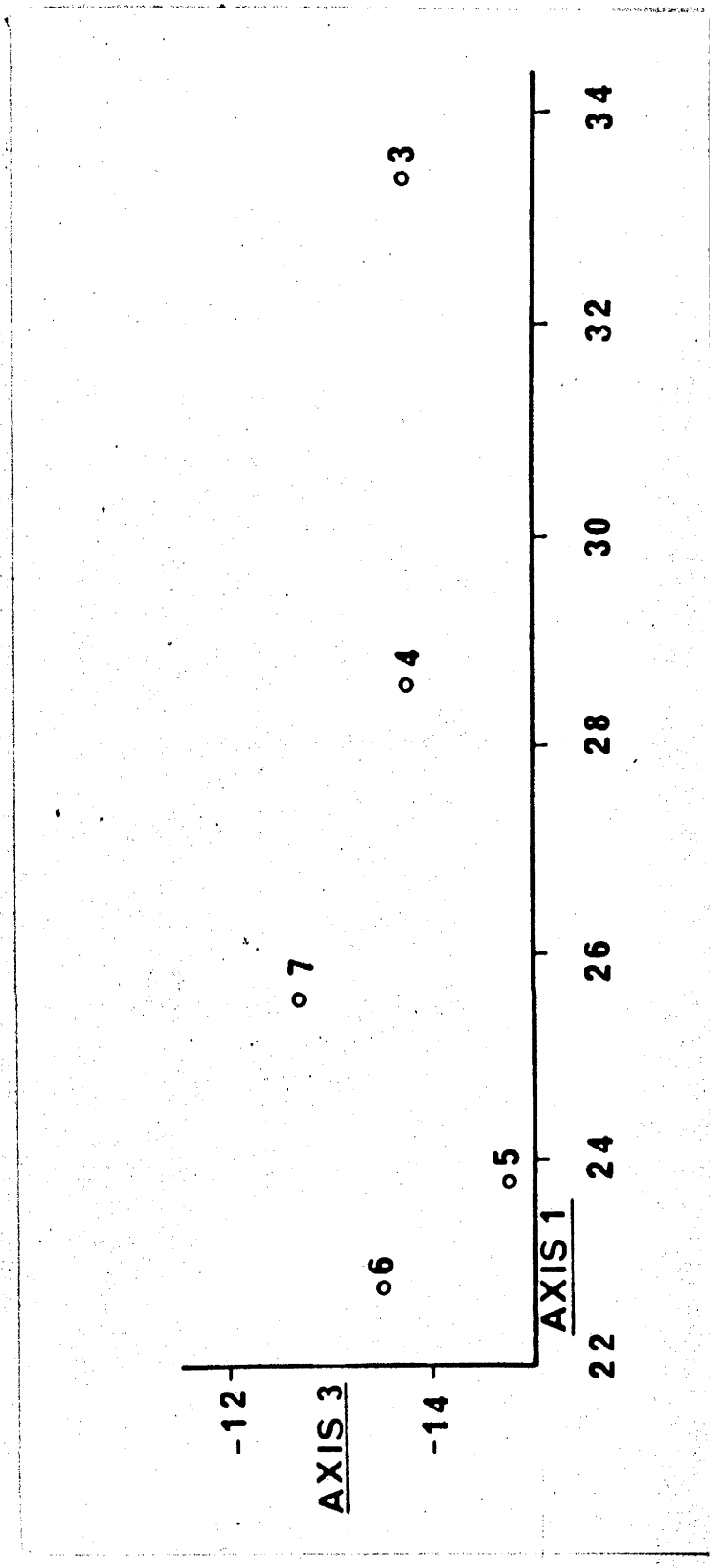

Fig. 13(b). Axes 1 and 3. Pinus nigra var. maritima. Temporal analysis of selected litter chemical concentrations. Mean canonical points of FH layer samples.

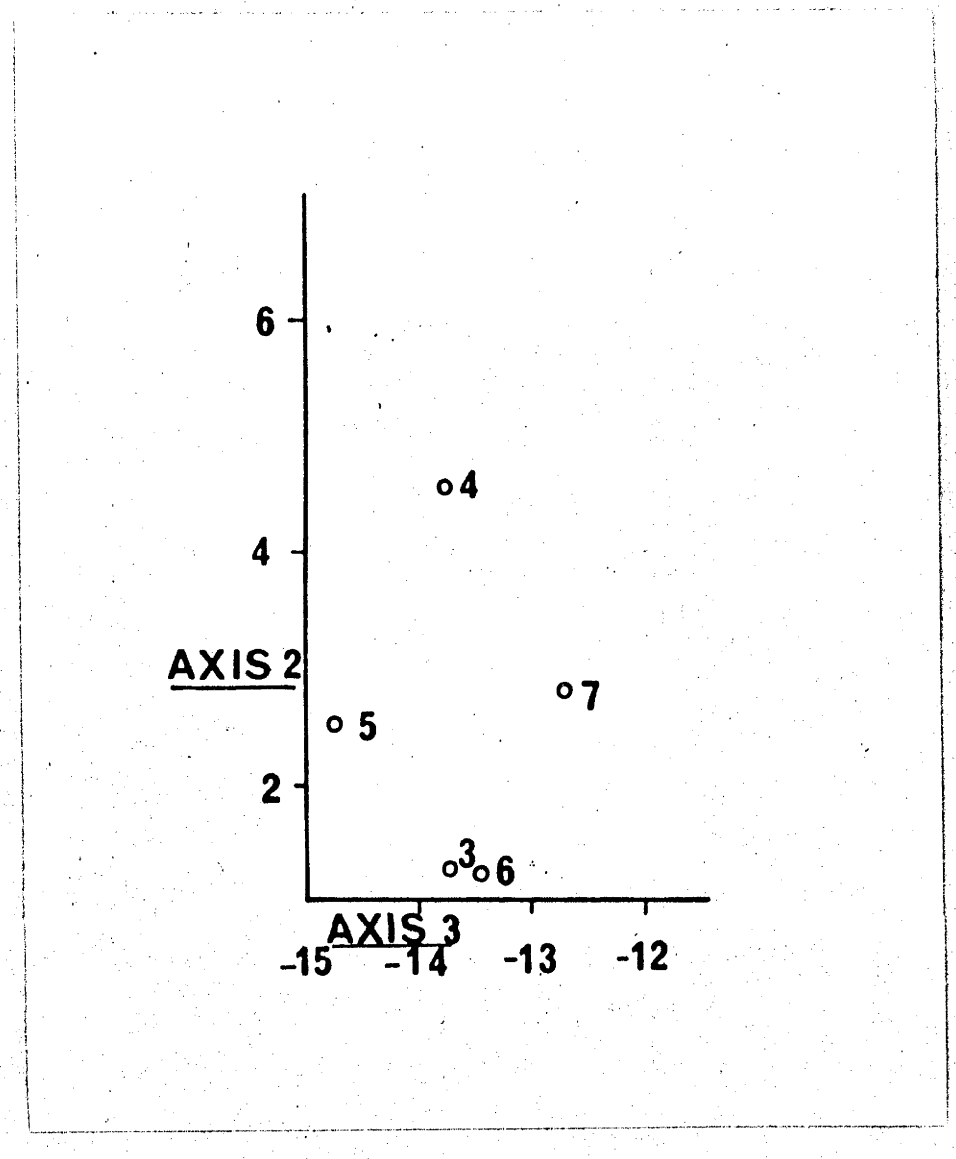

Fig. 13(c). Axes 2 and 3. Pinus nigra var. maritima. Temporal analysis of selected litter chemical concentrations. Mean canonical points of FH layer samples.

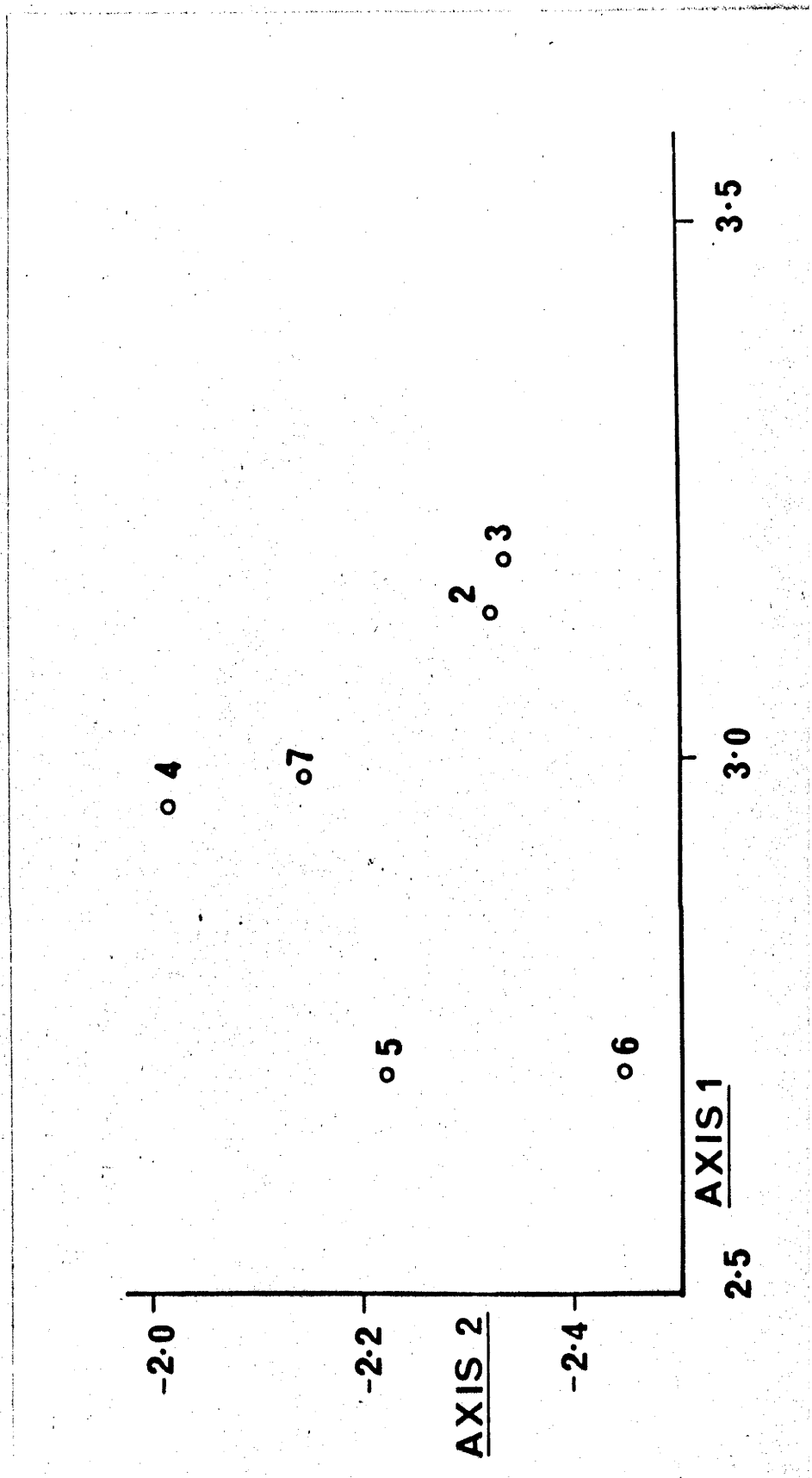

Fig. 14. Pinus nigra var. maritima. Temporal analysis of selected litter chemical weights. Mean canonical points.

CHAPTER SIX

THE EFFECTS OF CARBARYL AND DDT ON THE LITTER FAUNA OF A CORSICAN PINE STAND. A MULTIVARIATE COMPARISON

Biocidal compounds are currently required to reduce pest populations, despite their inimical effects on non-target organisms, other system elements and the general biosphere. They also have a largely untapped potential as ecological tools in the planned manipulation of animal and plant populations (Moore, 1967).

If adequate knowledge of both biological systems and their reaction to biocides were available, the differential toxicity of these compounds to the component taxa could be utilised to alter the system, or selected of its taxa, in a preconcieved way. As yet, their use in this way is restricted by their diverse effects on system interrelationships, their broad spectra of toxicity and often lengthy persistence times.

Biocides of all types are applied to ecological systems, not individual elements and the environmental consequences of their application are imperfectly understood, even for the so called 'target organism'. The introduction of integrated control programs in certain agricultural ecosystems marks the beginning of an ecological approach to utilisation of biocidal compounds through their more specific use. Some degree of

'ecological' specificity has been attained in various agricultural systems through the application of biocides at such times or places that the natural controlling agents are less likely to be affected than the target organism. Also, pesticides with narrow spectra of toxicity have been used with some success in manipulating the limited fauna of orchard populations (Sanford and Herbert, 1970). In highly diverse 'natural' systems this procedure is likely to have a more restricted potential. One possible exception is the use of relatively specific attractants such as insect pheromones, in conjunction with broad spectrum insecticides.

The soil is the eventual repository for a considerable proportion of the biocides applied to terrestrial ecosystems and, with the widespread use and low degradation rates of many of these compounds, it is of considerable importance to have detailed knowledge of their differential effects on taxa within treated ecosystems. Certain information is available for various arable and pastoral ecosystems, considerably less in the case of forest soils.

The emergence of a successful pest insect in the exotic conifer forests of Australia, either through immigration or successful adaption of an indigenous species, could lead to large scale aerial application of insecticides to protect the economic investment. Much of the applied chemical finds its way to the forest floor (Woodwell and Martin, 1964) and possible interference with the organisms involved in nutrient cycling makes it important to have information on the magnitude of the effect on, and likely recovery

times of the soil and litter fauna.

Experimental studies of the rôle of mesofauna in litter breakdown have been limited by lack of techniques for controlling the balance of litter animal taxa. Insecticides are potentially capable of providing this control (Edwards et al., 1969) but their effects must be well known for the environment under study. If this information can be obtained, powerful selective pressure may be exerted on an ecosystem to alter the taxonomic balance in some predetermined way. The results of this have been observed in the altered degradation rate of a natural substrate (Edwards, 1965) and this correlated with the emerging dominance of certain taxa.

Two pesticides, carbaryl and DDT, were applied at two dosage rates to the forest floor of the Corsican pine stand (Pinus nigra var. maritima) used for the preceeding studies. By sampling at intervals post application it was hoped to assess the differential effects on the exposed taxa and the nature of the recovery processes. DDT and carbaryl were chosen to contrast the effects of the chlorinated hydrocarbon with the less persistent carbamate, considering their spectra of toxicities and the different recovery rates likely to be induced. DDT also provided a reference chemical since its effects in the Australian environment could be compared and contrasted with those recorded by Hartenstein (1960) and other workers overseas.

METHODS

EXPERIMENTAL DESIGN

A one way unreplicated design was chosen for the experiment. Six plots five metres square were laid out in a block of two rows of three. An untreated area one metre wide was left between all plots to prevent inter plot contamination and allow comparable chances of recolonisation. Assignation of treatments to plots was random.

The treatments applied to each plot (Table 41) consisted of an approximately 'commercial' rate of application and another at ten times that level. All chemicals were applied with a knapsack sprayer, the plots being treated systematically in strips until the required quantity was applied. A small quantity of a non-ionic detergent was used as a wetting agent.

SAMPLING

Sampling was conducted on five occasions. These comprised one pre-treatment sample, one ten days after application and three more at approximately three monthly intervals (Table 42).

The pre treatment sample was taken to test the homogeneity of the original fauna of the plots. Ten cores were taken from each of the four corner plots of the design and counts of selected taxa were made. A canonical variate analysis of the data indicated no significant differences

between plots. The data were then pooled to give combined estimates of variable means and confidence limits for the taxa assessed.

Individual cores were 10 cm. by 10 cm. in size and comprised the litter layers and approximately 2.5 cm. of the underlying mineral soil. On removal from the sampling device cores were placed in individual plastic containers. These were sealed with a close fitting lid to prevent dessication and possible loss of animals in transit.

On return to the laboratory, all cores were held in a cool room at 2°C. until required for extraction. This was never longer than two weeks and usually considerably less. Edwards (in Johnson, 1967) has shown that soil cores may be stored at these temperatures for as long as a month without seriously affecting the extraction.

EXTRACTION AND COUNTING

The animals were extracted in modified, multiple Tullgren equipment fitted with vertically sided funnels. The repellent stimulus was the light and heat from a number of 60 watt light bulbs. Energy output was controlled by a variable transformer. The lower chambers of the extractors were provided with two large trays of constantly changing cold water to provide a humid atmosphere and stable temperature.

The extraction régime combined a constantly increasing repellent stimulus in the upper chamber with a relatively invariant state in the lower. The process of extraction

extended over seven days leading to a final temperature difference between the chambers of approximately 35°C. Animals emerging from the cores were fixed in a saturated aqueous solution of picric acid and later counted in dishes over a grid using a dissecting microscope.

RESULTS

DATA SUMMARIES

Geometric means and confidence limits are given for all samples.

The total numbers of animals, insects, mites and the sampling intensity (n) for all samples are presented in Table 43. Sample statistics of eleven selected taxa, for all sampling occasions, are presented in Tables 44 and 45. Asterisks in the tables denote that 95% confidence limits for the parametric mean include zero.

Data from the present study were analysed by the two methods discussed below. These analyses were computed for the taxa listed in Table 45 except that the immature and imaginal Coleoptera were combined to form one variable and the Araneae and Chilopoda were deleted.

All data were analysed as their natural logarithims, plus one.

CANONICAL VARIATE ANALYSIS

CVA were computed for the data from each post-

application collection sample and also on a combined basis treating the problem as one of twenty groups. Although this latter analysis is not rigorous, its results may be used to suggest possible relationships and considerations for further study (see also Tukey and Wilk, 1966). Significant eigenvalues ($P<0.05$) and the proportion of total variance explained by each are presented in Table 46.

The vectors associated with each useful eigenvalue are presented in Table 47 as normalised discriminant function coefficients. Table 48 presents the same eigenvectors whose elements have been multiplied by the square roots of the appropriate elements of the 'within' matrices to show the relative contributions of the individual variables to the discrimination.

Plots of sample mean canonical points are presented for each analysis in Figs. 15 to 19 for all useful roots.

SIMULTANEOUS TEST PROCEDURE ANALYSIS

Simultaneous test procedure analyses were carried out for each post application collection. All combinations of samples with eight variables simultaneously and for each variable alone were computed.

Maximal acceptable sample combinations ($P<0.05$) with all eight variables are presented in Table 50. Table 51 presents the results of the analysis of all possible univariate hypotheses. Non-significant subsets of samples are erected at the $P<0.05$ level.

INTERPRETATION AND DISCUSSION

MULTIVARIATE ANALYSIS

The multivariate analysis allowed a satisfactory resolution of sample differences. Unfortunately, no multivariate analyses of pesticide treated populations appear to have been published and no comparisons are possible.

CVA reduced the data to two or three useful dimensions in all cases and exact tests of the significance of sample differences were computed using Gabriel's (1968) STP. The contribution of the CVA lies partly in its graphical presentation of results allowing ready recognition of sample affinities and relationships.

At the first post application sampling, the treatment effects were not fully expressed since the insecticide treated populations had not diverged to any great extent from each other. However, all were different from the untreated population. The lack of significant difference between the carbaryl treated populations suggests this chemical and the higher DDT treatment initially caused a severe and possibly generalised reduction in the treated populations. At the lower DDT levels a more selective effect became apparent. By the time of the second post application sampling the populations had diverged sufficiently for them all to be significantly different. Although no non-significant groupings were present, populations from the lower treatments of both compounds

were closer to those of the untreated plots than those of the more heavily treated plots. Also, for both insecticides, the more heavily treated populations were closer to the less heavily treated populations than any other. This situation remained unaltered during subsequent sampling occasions. Little variation from this pattern was evident at the third sampling occasion except that the population of the low carbaryl treated plot had converged with that of the untreated plot to the point that they were no longer significantly different. At the final collection period the populations had diverged enough to be again significantly different from one another, due possibly to seasonal effects.

The combined analysis suggests that, except for the results of the first post application sampling, treatment effects are more important than those of the seasonal cycle since samples from each treatment resemble each other more closely than others of the same sampling occasion.

The best discriminator in the first two analyses was the Collembola. This is not suprising since treatment effects on this taxon were marked. In the third and fourth post-application analyses the Mesostigmata proved to be the best discriminating variable although the Collembola still remained high.

An interesting feature of the CVA is the importance placed on the Cryptostigmata as a discriminating variable despite its lack of significant variation in all analyses. See Cooley and Lohnes (1962) for a discussion of this problem.

UNIVARIATE ANALYSES

The non-significant subsets of means erected in Table 50 imply that those samples enclosed by the lines are not significantly different at $P < 0.05$. Certain taxa appear to be relatively unaffected by the treatments although the effects on lower level taxa may have been confounded by the relatively high taxonomic level used. The reactions of the individual taxa to the treatments applied are considered below.

Coccoidea

Treatment effects on the members of this taxon were small, especially at the lower dosage rates. DDT in particular showed only a slight effect at the lower level of treatment but both chemicals significantly decreased numbers at the higher rates. A suggestion of recovery from the effects of both compounds is apparent in the results for post application samples three and four.

Little information appears to be available about insecticide effects on soil dwelling Coccoidea beyond a statement in Edwards (1965) that DDT treatments cause a moderate reduction in Hemiptera.

Coleoptera

Data from the present experiment suggests the effect of carbaryl on soil dwelling Coleoptera is small as only

one significant difference was noted between treated and untreated populations. This slight effect of carbaryl is confirmed by Voronova (1968).

In contrast, DDT caused a marked reduction in numbers substantiating the findings of Edwards (1965). No significant dosage effect was noted for either chemical.

Collembola

Carbaryl treatments at both levels caused a marked and significant reduction in collembolan populations. Differences between the lighter and heavier dosages were significant for both chemicals. Aspok and An der Lahn (1963, in Edwards, 1965) reported that carbaryl treatments caused a marked depression in numbers of Collembola.

DDT had a different effect. Treatments at the lower level caused an initial depression in numbers followed by an increase over the untreated populations which rose past the point of significance in the final sampling. The heavier levels of DDT caused a longer term reduction in numbers and, at the end of the experiment, Collembola were still less numerous than in the untreated plots.

Moderate to large increases in the density of collembolan populations following the application of DDT have been recorded by a number of authors (see, inter alia, Baudissin, 1952 in Satchell, 1955; Edwards, 1964 and 1965; Edwards, Dennis and Empson, 1967; Hartenstein, 1960; Hoffman et al., 1949; Knight and Chesson, 1966; Sheals, 1956) for both arable and forest systems. This process is

probably directly analogous to the secondary outbreaks sometimes experienced in agricultural insecticide practice due to a reduced predator and parasite pressure. In soils this largely results from the differential toxicity of DDT for Collembola and mesostigmatic mites (Sheals, 1956; Edwards, 1965), a thesis supported by the results of the present experiment.

Diptera

Carbaryl appears to have little effect on Diptera and, although some disturbance to numbers was apparent, no constant effect was noted beyond a small and mostly non-significant depression in all cases. However, Voronova (1968) records that, 14 months after application, Diptera were still reduced by carbaryl treatments in comparison with untreated areas.

The effect of DDT did not appear to be large although the heavier doses had a depressing effect on numbers. Edwards (1965) reports that DDT causes a moderate reduction in numbers of soil Diptera.

Cryptostigmata

The Cryptostigmata appear to be little affected by any of the treatments applied and no significant differences were noted between populations at any of the post application sampling occasions.

In the case of carbaryl, this accords with Edwards

(1965) who states this chemical has no effect on numbers of saprophytic mites. In contrast, Voronova (1968) found a continuing depression in numbers of Cryptostigmata 14 months after application.

Edwards (1965) reports DDT causes a large reduction in numbers of saprophytic mites. This was not demonstrated in the present study.

Mesostigmata

Data from the present study suggests DDT severely depresses populations of soil dwelling Mesostigmata and that a significant effect of dosage exists. This confirms the observations of Edwards (1964, 1965), Edwards et al. (1967), Hartenstein (1960), Sheals (1956) and others.

Carbaryl has a somewhat less severe effect and populations treated at the lower dosage levels were not significantly different from those of the untreated areas. The heavier dosage rates do cause some further depression but recovery appears to have been effected by the final collection period. This does not conform with the claim by Edwards (1965) that carbaryl has no effect on members of this taxon.

Prostigmata

The treatments had little effect on soil dwelling Prostigmata although some slight depression may have been caused by the higher levels of DDT. However, the only

significant difference found between the populations of the untreated plots and all others was with that treated at the higher level of DDT.

There appears to be little information on the effects of these insecticides on soil dwelling Prostigmata.

Symphyla

Except for the first collection, both carbaryl and DDT caused significant reduction of treated populations at the heavier rates of application. At the lower level carbaryl treated populations were not significantly different from the check plot at any stage. DDT appeared to cause the greatest reduction to the population of Symphyla which accords with Edwards (1965) statement that DDT causes a moderate reduction in numbers. There appears to be little information about the effect of carbaryl on symphylid populations.

DISCUSSION AND CONCLUSIONS

In the sense of reversion to the status of the untreated population, no recovery was noted. This could not be expected to be completely fulfilled until after the biocides had largely degraded; a lengthy process in soils rich in organic matter. Given the dynamic temporal variation of most biological systems the pretreatment state is unlikely to be ever regained. Even if recovery were effected in terms of population numbers, a qualitative change would

probably still remain because during the period of pesticide breakdown, the population of the treated area will be growing from a combination of immigrants and those few individuals that were able to survive exposure.

In practical terms, the recovery process must be conceived of in a fairly broad way as a return to approximate comparability of treated and untreated populations in the ratios and absolute numbers of the major taxa of the system at each trophic level. The time scale required for even this practical conception of recovery to occur must inevitably be lengthy since it involves a complex superimposition of the population recovery trend occuring concurrently with biocide degradation on the normal seasonal cycles, oscillations due to differential toxicity and a possibly altered genetic structure. Immigration has an important bearing and the magnitude of its effect will be to help speed the recovery process through the expansion of populations in untreated pockets and provide an alternative population source to the survivors of the treatment. However, little credence can be placed in the statements of those who regard the effects of large scale biocide application as unimportant or short lived.

Because of the complexity of ecological systems and the taxonomic problems involved in the identification of many invertebrates at the species level, investigations of the nature of the present must usually be made on the basis of higher level taxa. A possible result of this may be the confounding of effects on certain apparently unaffected taxa. However, there appears to be large enough group

differences in susceptibility to most biocides for relatively high level taxa to be used. In attempting to assess both biocide effects and recovery, it is important to select taxa representing a broad range of trophic levels because only in this way can insight be attained into the wider and more long term effects of biocide action.

In spite of their long term and largely unpredictable effects on mixed species populations, it appears that at least the simpler agricultural systems could be manipulated in a limited way using current biocides. At some time in the future, a new range of narrow spectrum biocides, possibly tailored to affect only a given narrow range of genotypes, may become available and change much current thinking on pest control. In the meantime, limited use for experimental purposes such as suppression or promotion of certain taxa in soil organic matter breakdown studies has become quite feasible.

Multivariate analytical methods would appear to offer a particularly useful approach in studies of this nature since they can provide meaningful overall summaries in the complex problem of assessing interrelationships between populations.

TABLE 41. *Pinus nigra* var. *maritima*.
Pesticide treatments applied to the litter layers of each experimental plot.

Plot	Treatment Code	Biocide	Dosage ($g.ai./m^2$)	Formulation
1	b	Carbaryl	1.1286	80% wettable powder
2	a	nil	-	
3	d	D.D.T.	5.6043	25% miscible oil
4	e	D.D.T.	0.5604	25% miscible oil
5	a	nil	-	
6	c	Carbaryl	0.1128	80% wettable powder

TABLE 42. *Pinus nigra* var. *maritima*. Sampling dates and intervals in pesticide study.

Sample	Date	Interval
pre-application	5 November, 1969	0
application	17 December, 1969	42
1	28 December, 1969	11
2	2 April, 1970	95
3	14 July, 1970	103
4	28 October, 1970	106

Sample	n	Total Animals	Total Insecta	Total Acari
Prelim-inary	40	63794.3(55996.2-72676.4)	41778.2(35904.0-48610.7)	18169.2(15686.6-21042.3)
1 a	17	62259.0(49317.2-78589.6)	44384.6(33990.8-57949.0)	15210.4(12017.1-19245.2)
b	10	15389.4(9809.5-24111.4)	5777.6(3477.7-9556.0)	8448.7(5324.6-13371.9)
c	10	23228.6(14715.6-36633.1)	10550.1(6937.6-16017.2)	11861.0(7227.6-19424.5)
d	10	35759.8(24176.6-52869.7)	19747.5(12059.5-32296.1)	14813.3(10995.5-19947.8)
e	10	38243.5(28069.0-52092.9)	27350.7(19332.2-38677.7)	9029.9(6279.5-12966.0)
2 a	17	38218.0(30410.6-48023.2)	20608.5(15337.7-27678.8)	15654.6(12828.6-19098.2)
b	9	14407.2(10834.9-19146.4)	2609.0(1835.0-3692.8)	11048.8(8149.4-14965.2)
c	10	19912.7(14750.0-26870.1)	6207.5(4595.9-8372.2)	13009.6(10182.1-16614.5)
d	10	21338.4(16847.1-27020.1)	13216.7(9569.8-18239.1)	6992.8(4939.0-9883.7)
e	10	46859.4(32756.0-67016.7)	29943.2(19214.6-46631.4)	14929.8(11169.2-19945.3)
3 a	18	88205.9(71112.1-109403.0)	43690.1(32462.8-58788.3)	41286.5(35017.6-48674.5)
b	10	26688.9(21353.3-33351.5)	4048.3(3140.2-5211.0)	21791.7(16747.9-28345.4)
c	10	50808.6(36340.2-71021.4)	20272.6(12426.3-33033.9)	27695.3(20561.8-37291.6)
d	10	44365.3(31346.3-62774.2)	29384.4(20400.0-42306.3)	15119.4(10315.1-22139.9)
e	10	81326.8(60816.9-108742.1)	60538.9(43844.0-83576.4)	18957.7(14050.4-25566.8)
4 a	18	76510.9(66920.2-87474.1)	41932.0(33449.9-52558.4)	31458.8(28370.1-34882.6)
b	10	31236.3(22783.7-42811.1)	5217.3(3717.1-7307.1)	25404.1(18554.5-34768.6)
c	10	52657.0(40976.4-67659.0)	11307.0(8664.0-14747.1)	39925.8(29488.0-54045.8)
d	10	46979.8(33481.3-65904.2)	25868.4(17271.3-38720.1)	19570.1(13888.2-27559.8)
e	10	85209.7(64136.1-113196.9)	60167.8(44568.9-81213.9)	23899.0(17785.7-32101.6)

Table 43. Animal numbers in pesticide treated litter of a Pinus nigra var. maritima stand. Sampling intensity, geometric means and 95% confidence limits (individuals/m^2).

Taxon	$\bar{y}_g$ and 95% limits	Taxon	$\bar{y}_g$ and 95% limits
Coccoidea	185.0 (123.2-263.9)	Mesostigmata	6403.1 (5633.4-7276.2)
Coleoptera (imagines)	222.0 (168.9-285.6)	Prostigmata	767.2 (496.5-1160.7)
Coleoptera (immatures)	48.8 (27.7 - 73.2)	Araneae	385.2 (280.9-518.0)
Collembola	40061.4 (34289.0-46807.0)	Chilopoda	118.4 (76.5-170.3)
Diptera	604.1 (430.9-833.7)	Symphyla	207.8 (124.4-322.1)
Cryptostigmata	9665.7 (7857.5-11884.8)		

Table 44. Preliminary sample of Pinus nigra var. maritima litter fauna (individuals/m^2).

Sample	Taxon	Check Plot	High Carbaryl
1	Coccoidea	272.9(134.8-888.4)	90.8(6.8-241.0)
	Coleoptera (Imagines)	425.6(264.0-658.9)	137.7(59.6-254.0)
	Coleoptera (Immature)	54.0(16.0-104.3)	47.3(8.6-99.7)
	Collembola	42771.5(32500.5-56278.4)	5033.4(2971.8-8478.5)
	Diptera	350.9(248.3-483.7)	244.2(158.4-358.4)
	Cryptostigmata	5707.3(4355.7-7468.9)	3933.2(2556.6-6023.1)
	Mesostigmata	7239.5(5313.2-9851.2)	3688.9(1926.0-6985.9)
	Prostigmata	1335.6(960.2-1843.8)	305.3(112.2-674.4)
	Araneae	238.7(114.2-435.3)	222.7(90.9-445.5)
	Chilopoda	71.1(27.6-129.3)	102.4(36.5-200.0)
	Symphyla	872.1(587.9-1254.0)	359.0(155.2-725.3)
2	Coccoidea	847.8(456.8-1513.2)	157.0(23.3-435.8)
	Coleoptera (Imagines)	207.2(118.1-332.8)	379.1(214.9-628.9)
	Coleoptera (Immature)	41.9(8.3-85.9)	31.7 *
	Collembola	18185.1(13223.4-24994.8)	1621.3(1137.7-2293.9)
	Diptera	264.0(160.1-409.5)	173.8(59.3-370.6)
	Cryptostigmata	5855.3(4508.1-7596.2)	6237.9(4536.1-8564.4)
	Mesostigmata	8610.3(6988.3-10603.3)	3395.4(2148.2-5303.4)
	Prostigmata	631.5(375.3-1026.0)	846.4(367.8-1814.8)
	Araneae	360.6(251.0-504.4)	224.9(130.9-357.2)
	Chilopoda	114.0(31.6-248.0)	157.8(65.8-300.9)
	Symphyla	317.5(174.7-534.3)	47.0 *

Table 45. Animal numbers at each post-application sampling occasion. Geometric means and 95% confidence limits (individuals/m^2).

Low Carbaryl	High DDT	Low DDT
129.4(27.7-312.0)	137.7(53.6-267.9)	339.5(158.5-647.2)
153.1(51.9-321.7)	81.3(20.4-173.1)	76.2(20.2-158.2)
41.4 *	14.9 *	0.0 *
9819.7(6392.8-15055.3)	18910.6(11323.0-31538.3)	26323.1(18480.6-37475.8)
126.7(38.3-271.6)	243.7(155.3-362.9)	268.5(84.7-635.2)
5865.5(3379.6-10127.4)	6767.1(4703.4-9717.4)	4161.6(2917.6-5918.4)
5038.2(2928.2-8618.7)	6720.3(4720.0-9551.0)	3864.5(2174.2-6810.9)
564.8(362.1-856.4)	506.8(154.7-1345.8)	286.2(120.0-577.9)
155.0(55.3-319.0)	82.9(2.7-225.8)	81.3(42.4-130.9)
37.4(1.3-86.4)	62.4(16.2-127.0)	62.4(16.2-127.0)
388.9(163.2-808.3)	329.1(162.0-602.7)	491.2(185.7-1123.1)
162.9(53.3-350.6)	64.4(6.0-154.9)	1315.9(694.1-2424.4)
170.7(51.9-382.5)	37.4(1.3-86.4)	69.2(10.1-160.0)
0.0 *	7.2 *	14.9 *
5205.9(3747.3-7217.5)	12698.4(9095.0-17713.7)	27855.4(17671.5-43875.4)
160.5(81.9-273.1)	134.3(38.5-296.3)	197.2(97.6-346.9)
6623.7(5198.4-8432.3)	5642.5(4173.5-7616.5)	9157.1(6186.3-13531.7)
5231.3(2843.0-9557.7)	796.8(307.1-1875.4)	4515.2(3262.3-6237.8)
595.2(264.6-1225.6)	275.2(102.0-597.0)	740.3(522.0-1035.5)
253.2(133.9-433.5)	0.0 *	61.4(7.2-143.0)
94.3(36.9-175.9)	28.2 *	204.8(95.3-375.6)
223.4(98.7-426.2)	23.1 *	162.7(49.2-362.8)

Table 45 (cont.).

Sample	Taxon	Check Plot	High Carbaryl
3	Coccoidea	358.3(158.1-713.8)	181.0(65.7-382.3)
	Coleoptera (Imagines)	520.9(308.8-843.2)	86.6(14.0-205.5)
	Coleoptera (Immature)	289.6(173.4-455.1)	125.9(57.7-223.4)
	Collembola	41198.7(30466.3-55699.5)	3469.4(2645.5-4540.5)
	Diptera	449.9(288.5-678.2)	28.2 *
	Cryptostigmata	16298.4(13268.2-20015.6)	11184.8(8261.4-15130.2)
	Mesostigmata	16150.0(13138.0-19847.1)	7293.9(6101.7-8715.2)
	Prostigmata	2721.6(2030.3-3637.2)	2407.2(1093.9-5164.9)
	Araneae	264.7(136.5-462.6)	108.3(32.5-227.3)
	Chilopoda	241.9(142.7-381.8)	28.2 *
	Symphyla	357.3(219.1-555.4)	78.3(22.8-158.8)
4	Coccoidea	142.0(35.5-332.1)	207.5(87.5-404.3)
	Coleoptera (Imagines)	261.6(175.7-374.1)	64.4(18.7-127.7)
	Coleoptera (Immature)	37.0(11.0-69.0)	88.8(32.4-169.3)
	Collembola	40139.5(31719.5-50787.6)	4121.3(2719.9-6219.2)
	Diptera	533.9(335.4-822.8)	291.2(132.7-557.6)
	Cryptostigmata	10889.3(8885.2-13340.4)	12743.6(9395.4-17272.5)
	Mesostigmata	11290.3(9196.7-13855.5)	7762.7(4747.0-12654.7)
	Prostigmata	2995.0(2394.9-3739.3)	1844.7(1096.1-3062.0)
	Araneae	217.4(123.6-350.4)	157.4(28.2-416.8)
	Chilopoda	159.5(92.8-248.6)	85.4(19.8-186.8)
	Symphyla	349.6(182.1-616.6)	85.4(19.8-186.8)

Table 45 (cont.).

Low Carbaryl	High DDT	Low DDT
141.0(13.1-404.4)	11.6 *	444.4(186.0-936.0)
232.6(127.2-387.0)	31.9(2.1-70.4)	110.7(67.1-165.8)
74.1(27.2-138.2)	7.2 *	14.9 *
19238.9(11682.5-31641.6)	29389.4(20450.4-42246.1)	59449.3(42806.1-82548.1)
209.5(108.4-359.7)	47.3(8.6-99.7)	131.0(57.6-238.4)
12014.8(9041.6-15954.9)	11109.3(8099.6-15223.7)	13699.3(9794.1-19145.8)
11709.0(8483.3-16146.9)	579.6(213.8-1371.8)	2471.5(1763.1-3449.2)
3152.4(1903.6-5179.5)	1476.6(415.1-4726.0)	2170.8(1379.3-3385.7)
220.2(117.2-372.1)	0.0 *	14.9 *
150.5(49.5-319.6)	23.1 *	182.5(99.9-299.3)
174.4(49.3-406.2)	7.2 *	130.3(23.2-330.6)
51.5(7.2-114.4)	64.4(18.7-127.7)	334.9(233.6-466.8)
132.5(72.9-212.6)	14.9 *	14.9 *
37.4(1.3-86.4)		23.1 *
10294.6(7925.3-13363.5)	25543.3(17014.9-38321.3)	59037.0(43386.8-80319.4)
173.1(63.7-355.5)	108.3(47.8-193.5)	425.3(207.6-797.2)
10506.6(8422.6-13100.1)	16697.4(11708.1-23795.0)	14306.5(10640.7-19223.3)
14912.0(9087.4-24429.2)	785.7(477.0-1259.7)	2099.9(1218.7-3570.1)
4765.7(2808.0-8041.4)	1078.8(508.5-2183.7)	5156.7(3160.1-8375.9)
117.8(33.2-256.1)	0.0 *	0.0 *
88.8(32.4-169.3)	50.6 *	115.5(50.8-207.9)
157.8(59.6-316.4)	37.4 *	89.6(19.6-200.6)

Table 45 (cont.).

TABLE 46. Canonical variate analysis of animal numbers in pesticide treated plots. Significant ($P < 0.05$) eigenvalues and percentage variance explained by each.

Sample	Order	Eigenvalue	Percentage	Cumulative Percentage
1	I	3.3990	66.3115	66.3115
	II	1.3663	26.6554	92.9669
2	I	6.1089	66.1584	66.1584
	II	2.4478	26.5096	92.6680
	III	0.5034	5.4520	98.1200
3	I	9.5610	68.5079	68.5079
	II	3.9334	28.1846	96.6925
	III	0.3124	2.2386	98.9311
4	I	10.7777	70.3459	70.3459
	II	3.4134	22.2794	92.6253
	III	0.6418	4.1892	96.8145
	IV	0.4881	3.1855	100.0000
Combined	I	9.5549	51.0319	51.0319
	II	5.0125	26.7711	77.8030
	III	2.4504	13.0876	90.8906
	IV	0.8470	4.5235	95.4141
	V	0.3638	1.9433	97.3574
	VI	0.2687	1.4353	98.7927
	VII	0.1700	0.9077	99.7834

Sample	Root	Coccoidea	Coleoptera	Collembola	Diptera	Cryptostigmata	Mesostigmata	Prostigmata	Symphyla
1	I	0.2690	0.0101	0.7877	-0.4811	-0.2434	-0.0127	0.0071	0.1272
	II	-0.2444	0.7536	-0.1881	-0.0077	0.0160	0.4859	0.2902	-0.1280
2	I	-0.0344	-0.3110	0.8922	-0.1275	0.0170	-0.0696	-0.1856	-0.2241
	II	0.2557	0.1411	0.0913	-0.1147	-0.6063	0.6843	-0.0479	0.2345
	III	0.5263	0.2162	-0.0996	-0.0998	0.5178	-0.2193	0.2352	-0.5337
3	I	0.0233	0.1836	-0.6713	0.2318	-0.0096	0.6670	-0.0913	0.0893
	II	-0.1061	0.0855	-0.6407	-0.2353	0.6635	-0.2562	-0.0405	-0.0896
4	I	-0.0542	-0.1240	0.7243	0.0769	0.2508	-0.6154	0.0397	-0.0893
	II	-0.0668	0.1962	0.5545	0.1313	-0.7494	0.2483	0.0897	-0.0292

Table 47. Pinus nigra var. maritima. Canonical variate analysis of pesticide treated litter animal populations. Normalised coefficients for all useful discriminant functions.

Sample	Root	Coccoidea	Coleoptera	Collembola	Diptera	Cryptostigmata	Mesostigmata	Prostigmata	Symphyla
1	I	1.3362	0.0416	3.4409	-1.9701	-1.2163	0.0744	0.0380	0.5660
	II	-1.2139	3.1150	-0.8218	-0.0314	0.0802	2.8369	1.5562	-0.5697
2	I	-0.2143	-1.4223	3.4427	-0.5824	0.0550	-0.3420	-1.0765	-1.0848
	II	1.5930	0.6453	0.3522	-0.5242	-1.9622	3.3606	-0.2779	1.1353
	III	3.2786	0.9888	-0.3843	-0.4557	1.6756	-1.0770	1.3645	-2.5839
3	I	0.1577	0.7988	-2.6806	0.9501	-0.0296	2.7943	0.6089	0.4478
	II	-0.7175	0.3718	-2.5583	-0.9642	2.0463	-1.0735	0.2702	-0.4496
4	I	-0.3094	-0.4528	2.5472	0.3931	0.7495	-2.6845	-0.1929	-0.4780
	II	-0.3815	0.7162	1.9500	0.6731	-2.2401	1.0832	0.4354	-0.1561

Table 48. Pinus nigra var. maritima. Canonical variate analysis of pesticide treated litter animal populations. Scaled coefficients for all useful discriminant functions.

TABLE 49. Analysis of pesticide treated litter animal populations. STP analysis of all eight variable null hypotheses at each post-application collection interval. Maximal acceptable combinations of samples at P <0.05.

Collection	Sample Combination	θ	$\theta[0.05]$
1	b, c c, d	0.1712 0.2658	0.4289
2	*		0.4347
3	a, c	0.3019	0.4226
4	*		0.4226

* denotes all sample combinations significantly different at P <0.05

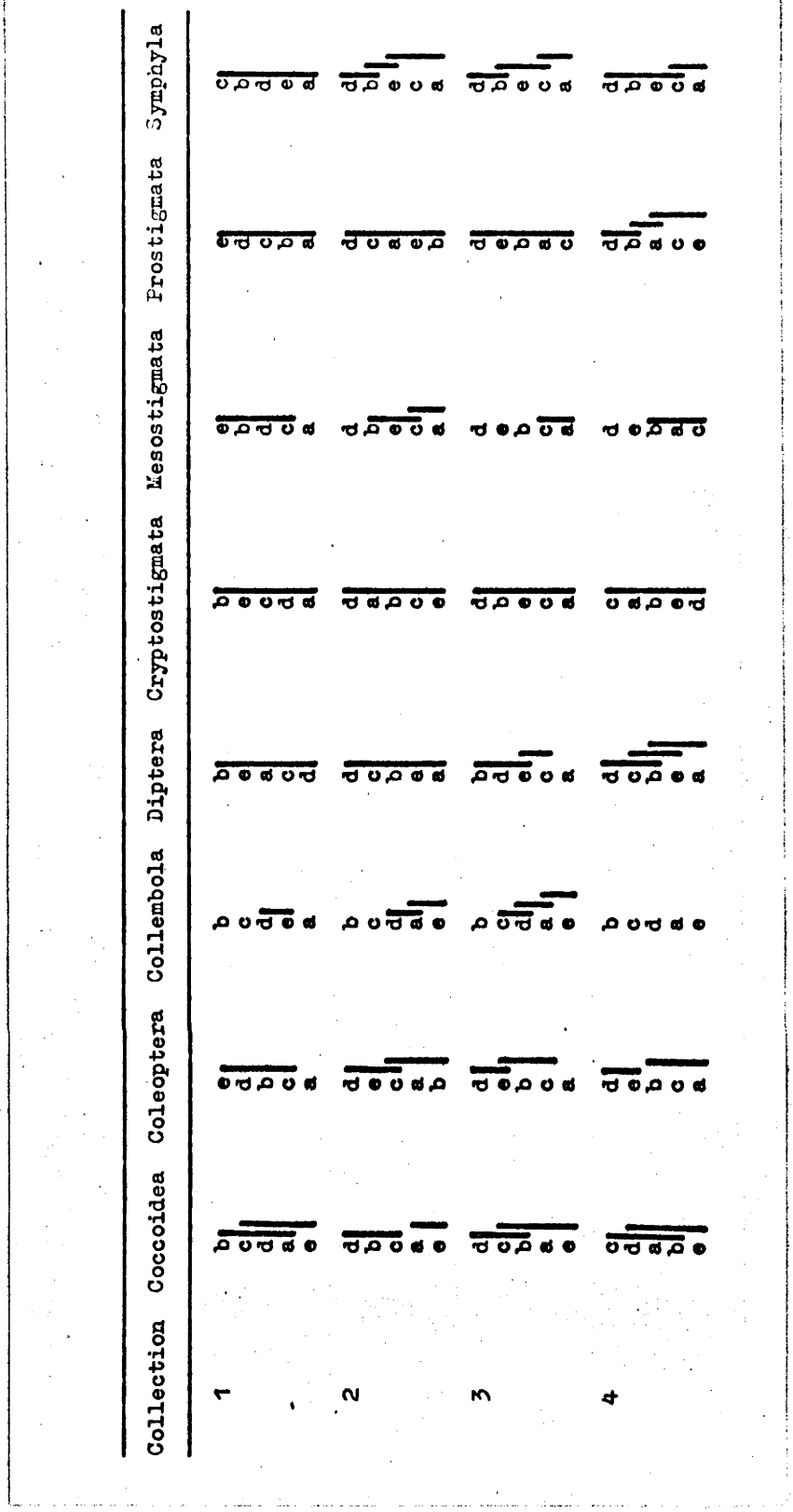

Table 50. Analysis of pesticide treated litter animal populations. Univariate STP analyses of all post-application collections. Non-significant subsets are at $P < 0.05$ and means are listed in increasing order.

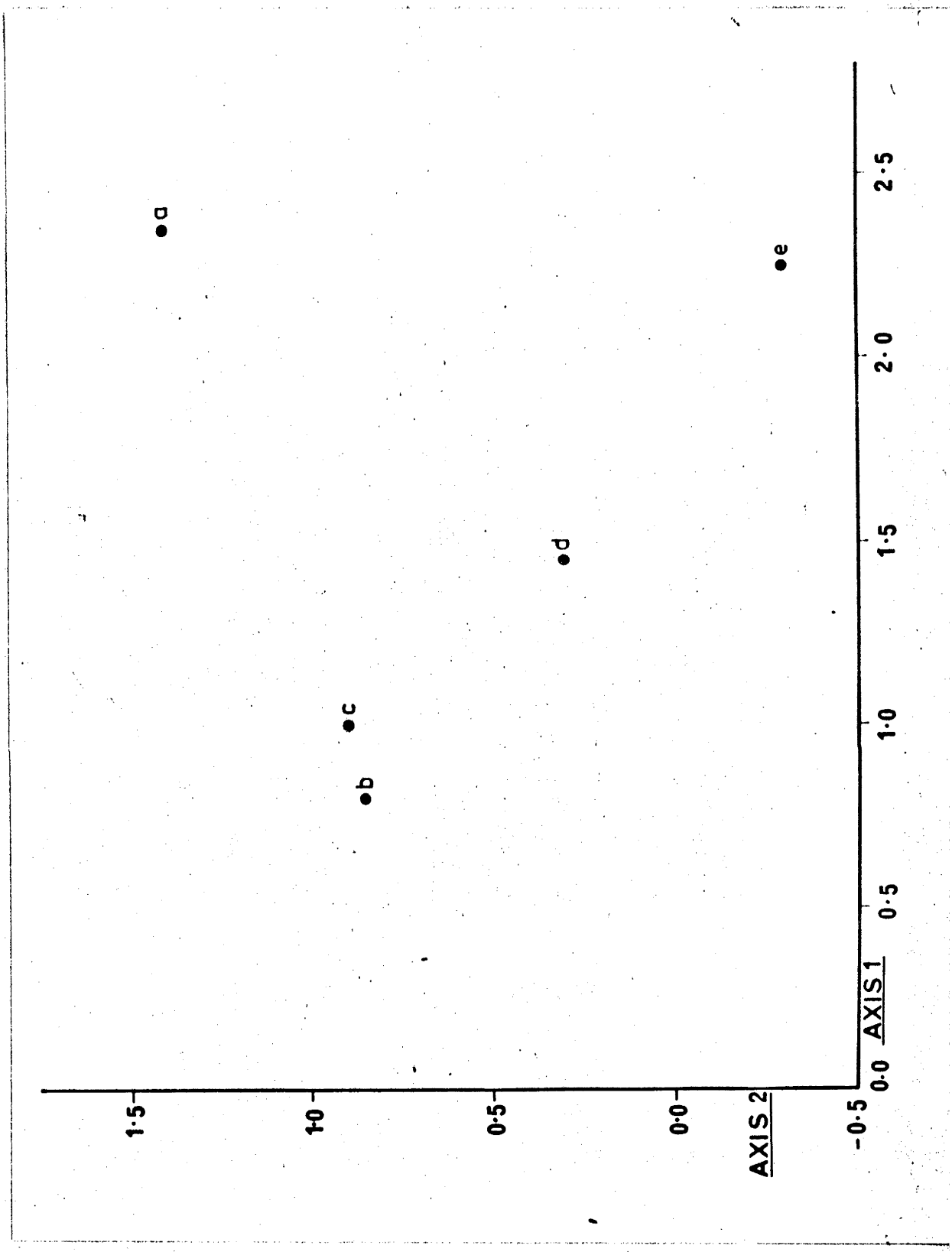

Fig. 15. Pinus nigra var. maritima. Analysis of insecticide effects on litter arthropod taxa. Sampling date 1. Mean canonical points.

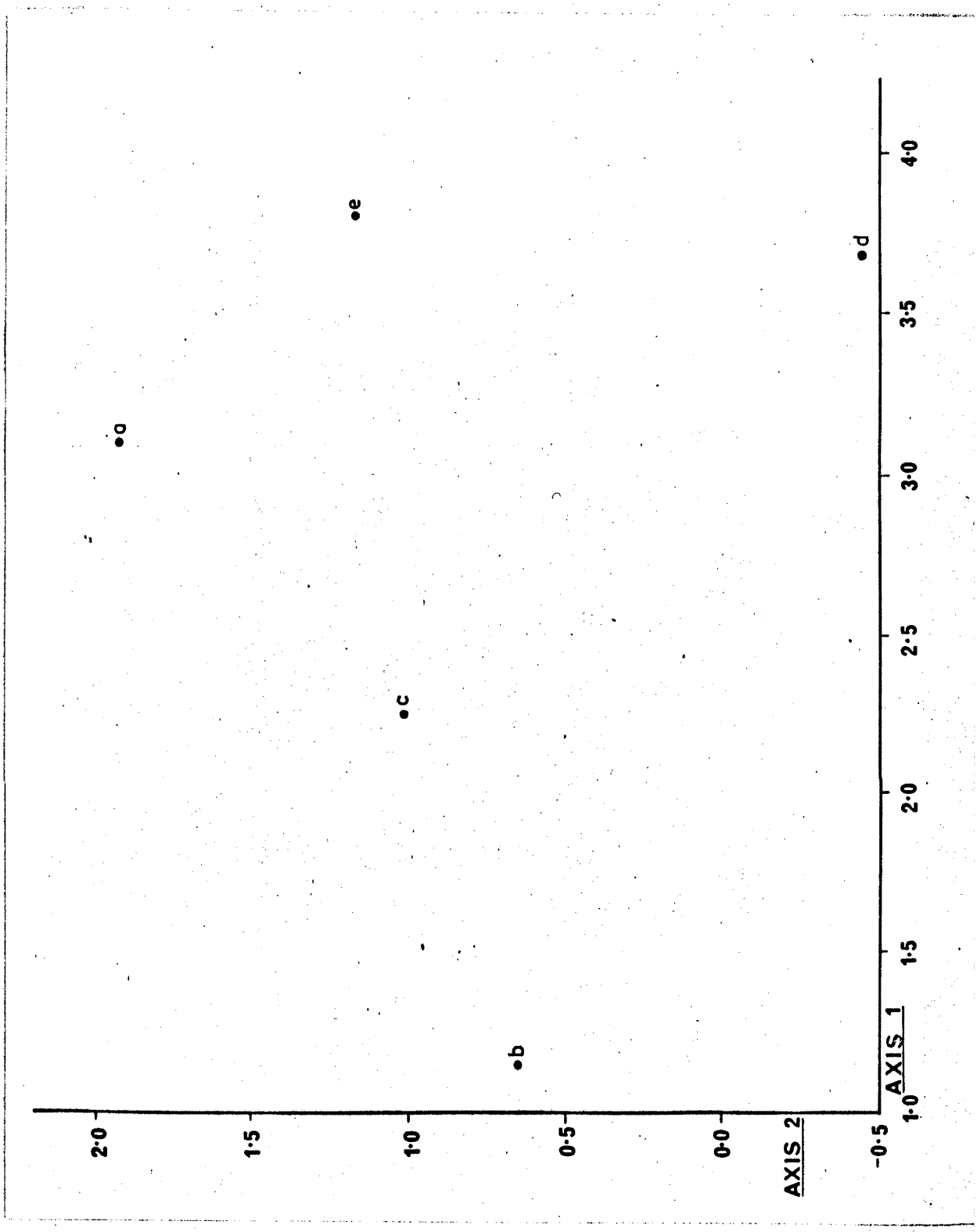

Fig. 16(a). Axes 1 and 2. Pinus nigra var. maritima. Analysis of insecticide effects on litter arthropod taxa. Sampling date 2. Mean canonical points.

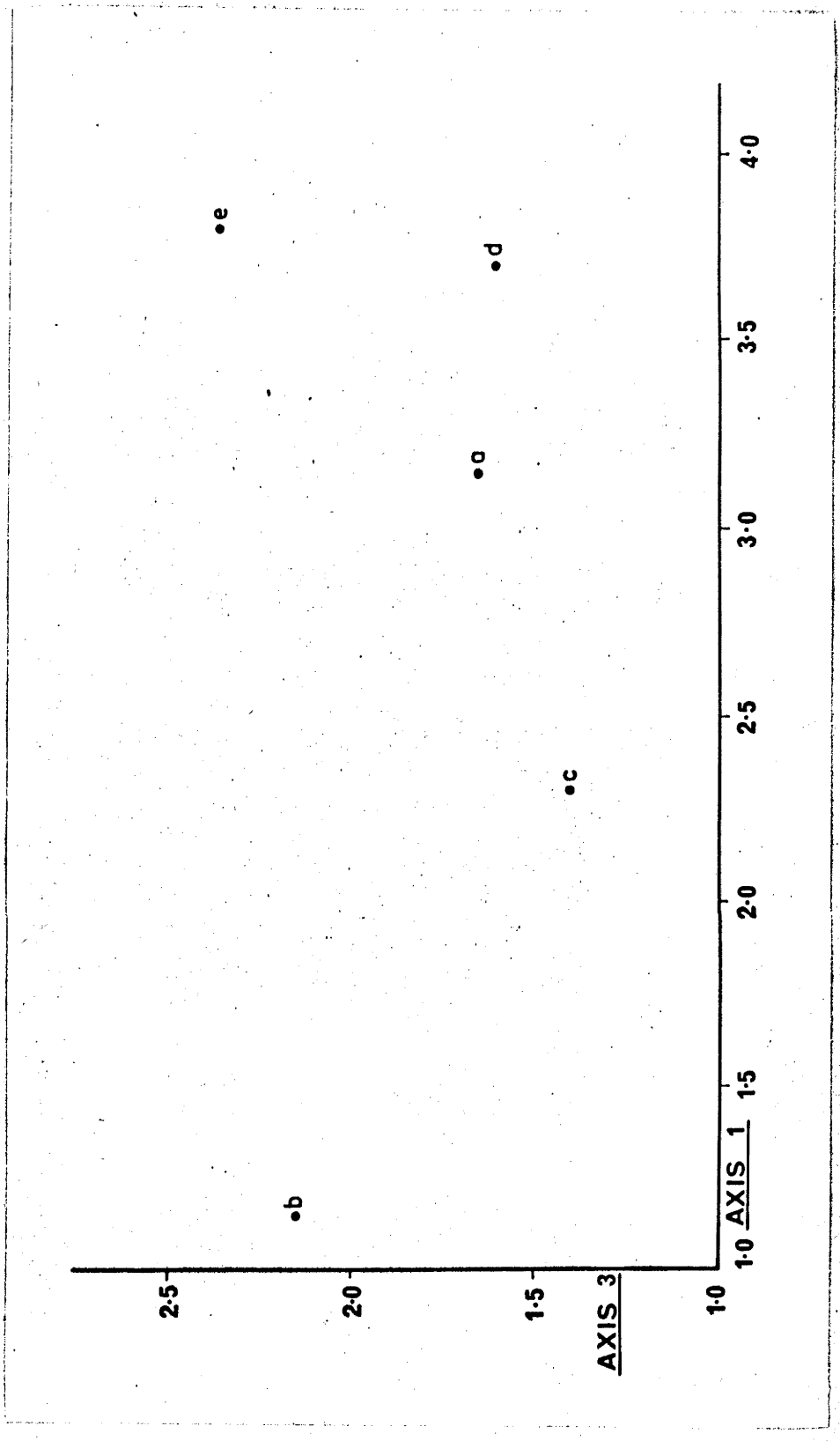

Fig. 16(b). Axes 1 and 3. Pinus nigra var. maritima. Analysis of insecticide effects on litter arthropod taxa. Sampling date 2. Mean canonical points.

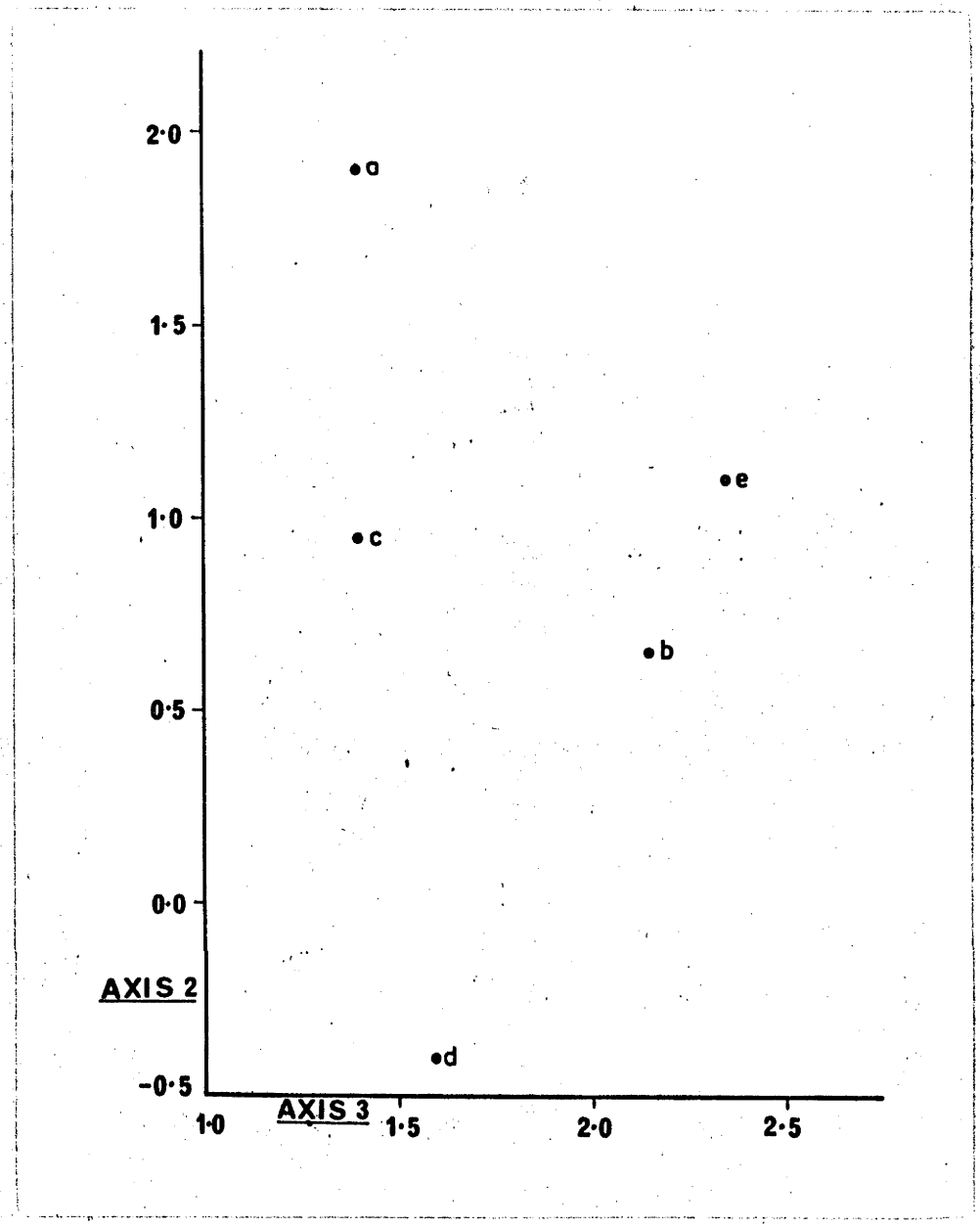

Fig. 16(c). Axes 2 and 3. Pinus nigra var. maritima. Analysis of insecticide effects on litter arthropod taxa. Sampling date 2. Mean canonical points.

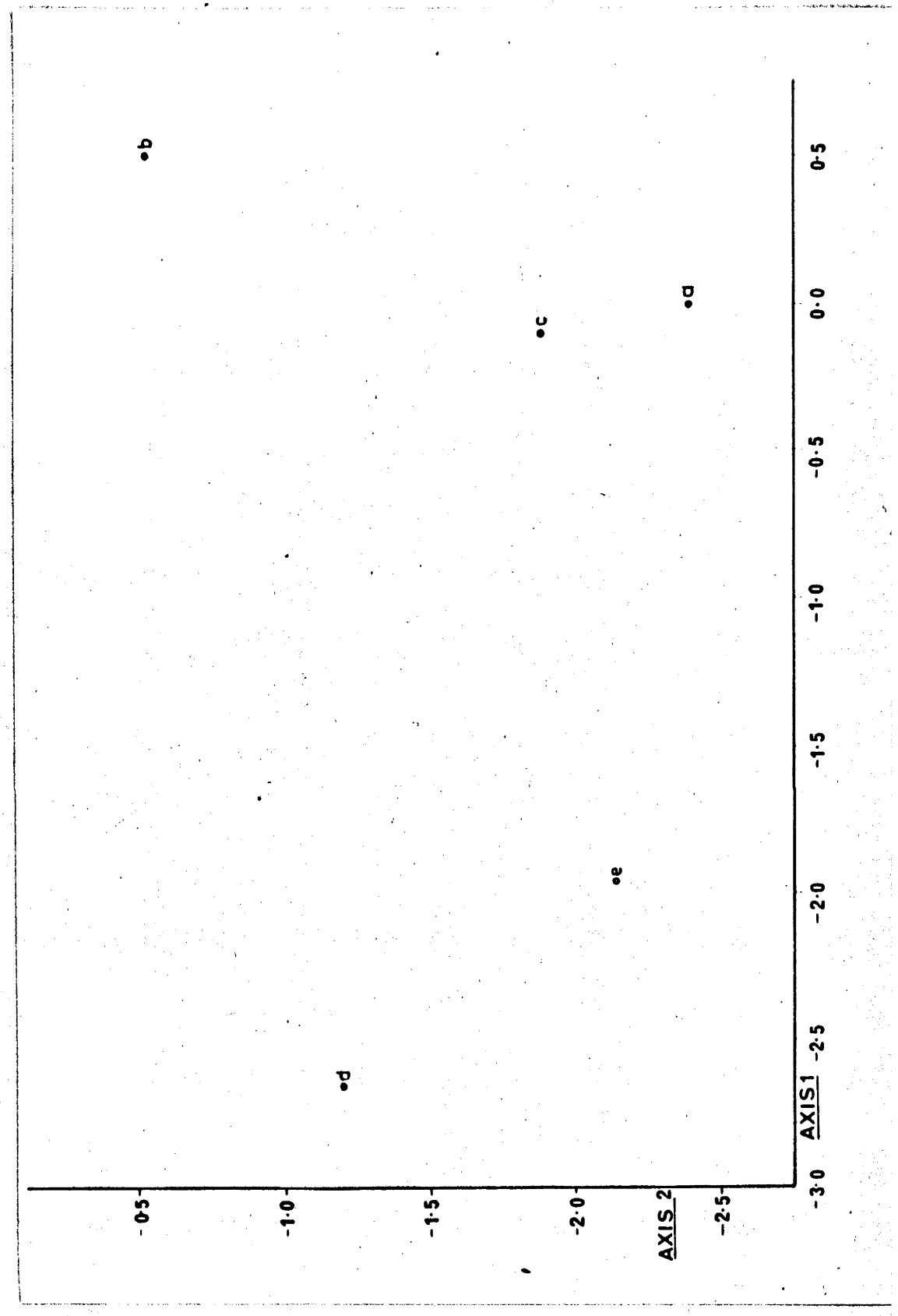

Fig. 17. Pinus nigra var. maritima. Analysis of insecticide effects on litter arthropod taxa. Sampling date 3. Mean canonical points.

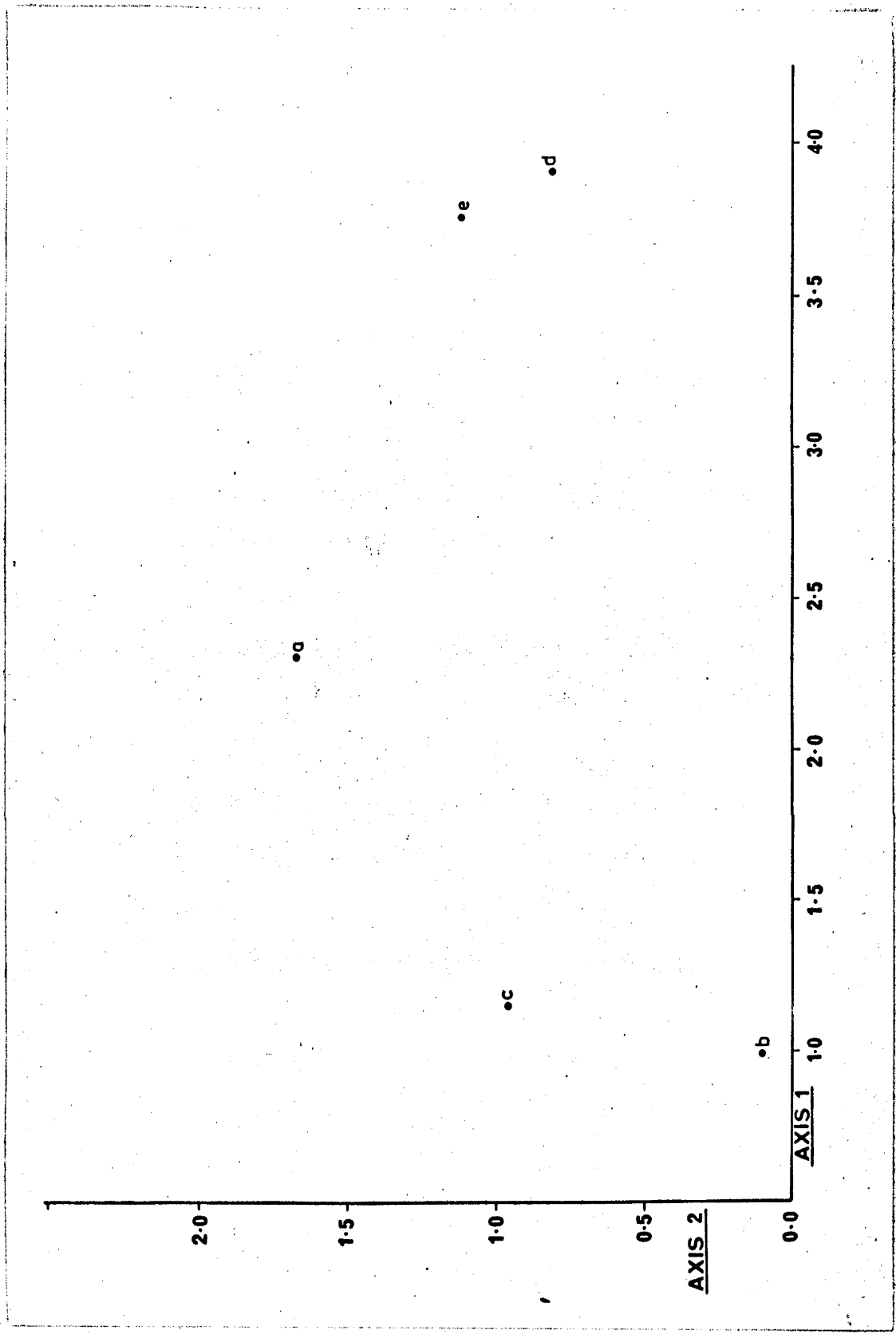

Fig. 18. Pinus nigra var. maritima. Analysis of insecticide effects on litter animal taxa. Sampling date 4. Mean canonical points.

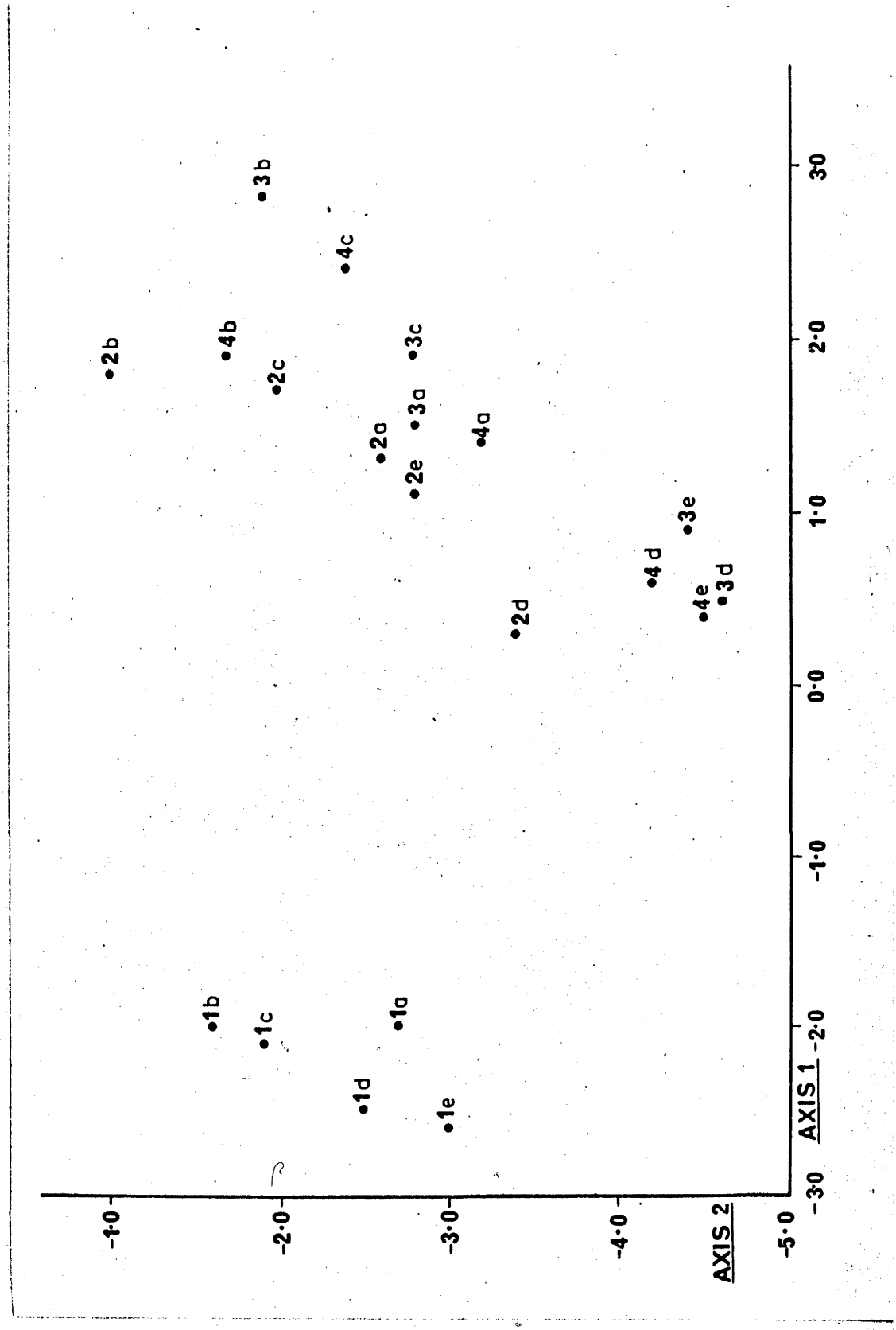

Fig. 19(a). Axes 1 and 2. Pinus nigra var. maritima. Analysis of insecticide effects on litter animal taxa. Combined analysis of all post application samples. Mean canonical points.

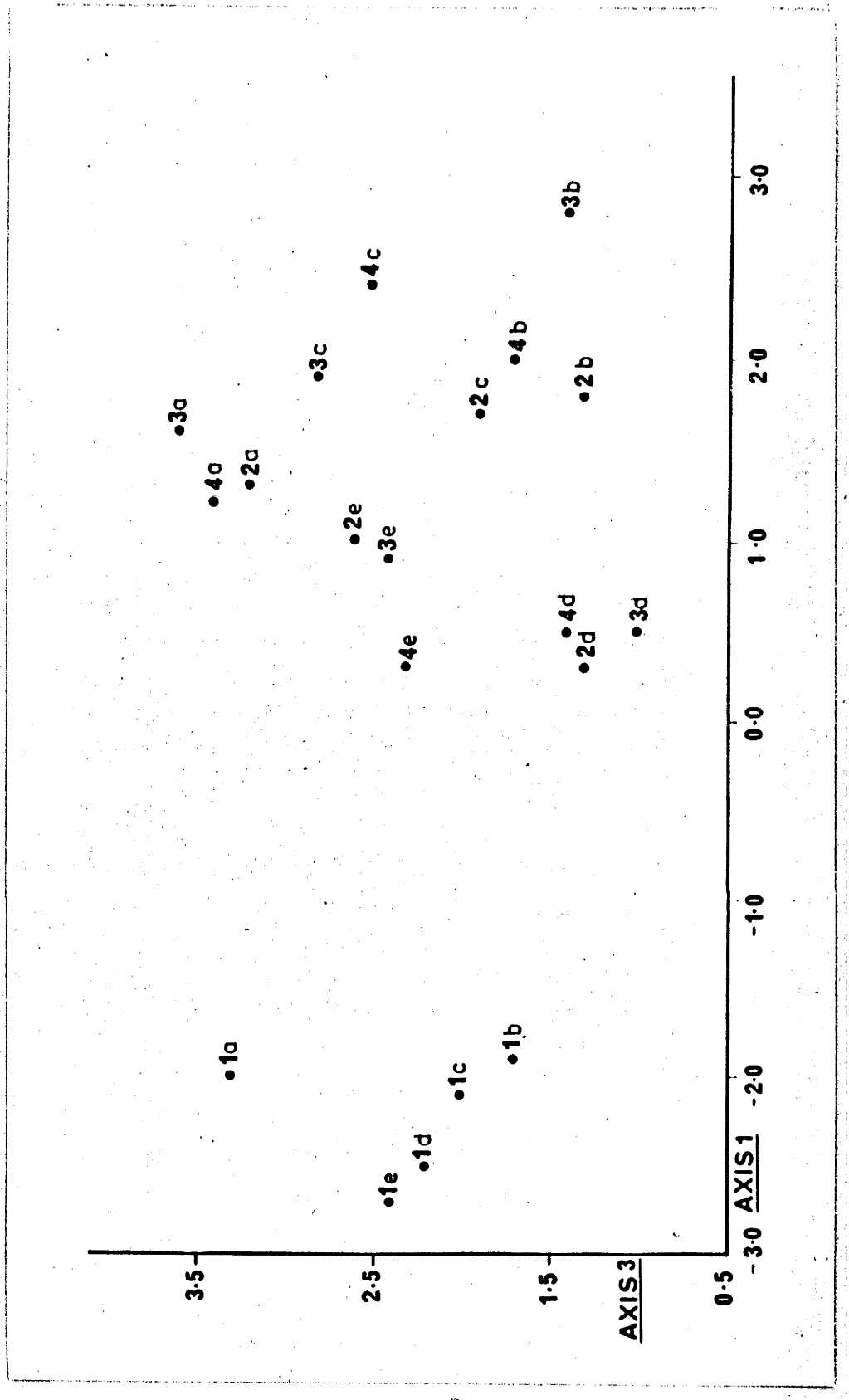

Fig. 19(b). Axes 1 and 3. Pinus nigra var. maritima. Analysis of insecticide effects on litter animal taxa. Combined analysis of all post application samples. Mean canonical points.

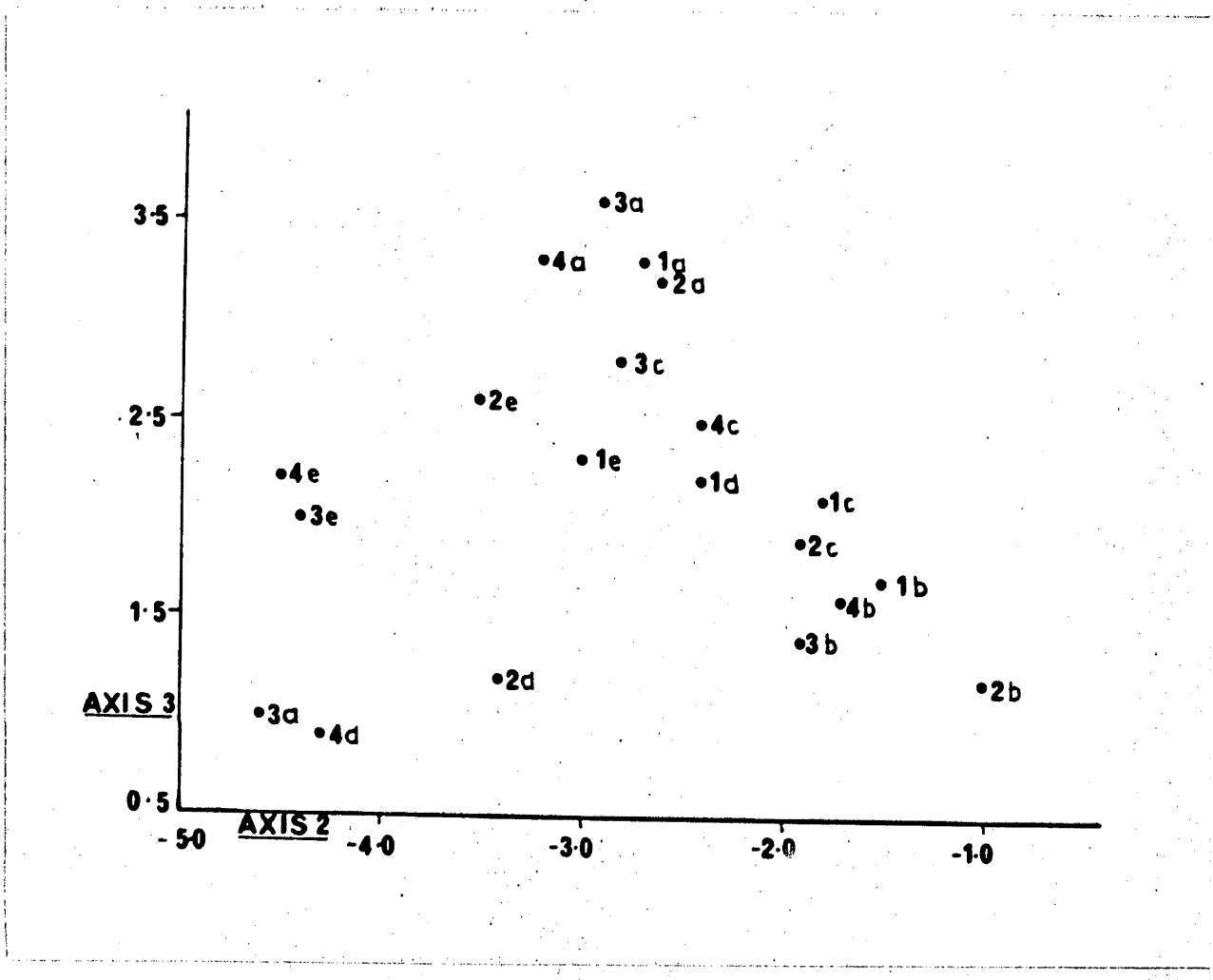

Fig. 19(c). Axes 2 and 3. Pinus nigra var. maritima. Analysis of insecticide effects on litter animal taxa. Combined analysis of all post application samples. Mean canonical points.

CHAPTER SEVEN

DISCUSSION AND CONCLUSIONS

LITTERFALL

Litterfall has been regarded as an index of productivity (Bray and Gorham, 1964) in spite of its subjection to a number of random and cyclical phenomena unrelated to the latter. Because of this, its use as a guide to productivity in conifer plantations must be limited to the comparison of means for several years fall in mature, closed-canopy forests and stands. Whatever its value in this regard, it is certainly one of the most influential factors in the development of forest soils and, consequently, entire forest ecosystems.

The magnitude of litterfall, in terms of total accession of organic matter and mineral elements, appears in all species studied to be within the range of results from other parts of the world although high quality Pinus radiata stands usually produce a greater mass of litterfall. In the case of Pinus lambertiana, no comparison is possible although results indicate that accession in this species is of the same order of magnitude as that of the other Pinus species. Certainly, in its chemical status and accession of mineral elements, this species appears to be close to members of the same genus.

Comparison of species suggests that the members of the

genus Pinus tend to form a discrete group separate from Pseudotsuga menziesii in most litterfall characteristics viz. total weight of litterfall, concentrations and weights of the plant nutrient elements measured. In spite of this general group affinity, statistically significant ($P<0.05$) differences showed up between the Pinus species for each interval and, because of the uniqueness of litterfall inputs from each species, long term development of ecosystems under the influence of any one tree species will probably be unique. Taxonomically similar species may also be expected to give rise to ecosystems that are closer to each other than to those not so related.

As might be expected, temporal variation in the measured characteristics of litterfall is marked. In all species, significant differences existed between sampling occasions except for two temporally adjacent samples from the Ps. menziesii stand. These were not significantly different ($P<0.05$) over the late spring-summer period in the weights of the measured elements accessed.

The pattern of litterfall accession has potentially important implications for sampling litterfall, litter and forest soils. Non random accession of litterfall has been recognised empirically (Ovington, 1954) but not characterised numerically. More work is required to enumerate relationships present and to discover if soil properties are reflected in the accession patterns of litterfall and leachates. The demonstration of correlation between dependent and independent variables in the study reported in Chapter Four suggests that, compared with

random sampling, stratified sampling plans based on size of tree and distance to Tree I may give more realistic biological assessment and reduce sample variance. For all characters, stratification will probably be most effective in species that shed their bark readily.

LITTER

The mor litter layers of conifer forests tie up large proportions of the total amounts of plant nutrient elements, organic matter and energy available within the ecosystems involved. It is thus of some importance to ensure that the magnitude and chemical composition of litter layers are known for any forest ecosystem under consideration.

The chemistry of resistance of mor litter to breakdown has been the subject of considerable study but is not yet well understood (Alexander, 1965). However, something is known of the masses of litter layers formed under various species and in a range of environments. From this, much can be inferred on the way in which litter accumulates although the mechanisms involved require considerable study for their resolution.

Litter layers in conifer plantations probably develop through a number of 'seral' stages until they attain an approximate equilibrium. This takes some time to develop and may depend partially on the vegetation type preceeding the current crop. Initially, needles fall around the bases of the seedling trees and often a continuous layer is not

formed for some years. Ground vegetation is progressively suppressed until, by canopy closure, it may virtually disappear. The litter layers may achieve an approximate equilibrium in terms of weight at some stage thereafter.

In terms of weight, this equilibrium is a dynamic balance between inputs from litterfall, leachates, aeolian deposits and outputs derived through leaching of inorganic elements and of material solubilised through the action of the saprobiota. The latter being constrained by its chemical environment, possibly through a feedback mechanism. This may operate through the organic influences of the changing nature of leachates and moisture status associated with the build up of the litter layers and development of the tree crop.

In terms of qualitative variation, the equilibrium considered above is possibly more apparent than real. Resistant inputs, such as lignins, degrade at a slower rate than others such as the simpler carbohydrates. Thus, over time, a build up of these resistant materials seems inevitable. At the microbiotal level changes occur which initially involve displacement of the indigenous biota by that subset capable of surviving under the altered conditions imposed by the new vegetational <u>régime</u>. At each 'sere' development of a characteristic saprobiota supercedes the previous until a true equilibrium is attained. This must inevitably be a lengthy process.

LITTER BREAKDOWN

It has been demonstrated that the breakdown of litter is best approximated by the sum of a series of negative exponentials (Minderman, 1968) corresponding to the various organic fractions of litter fall. It has also been shown that the concentrations of resistant fractions, such as lignins, increase over time in litter (Alexander, 1965). Thus, as litter does not appear to build up indefinitely, a stage of equilibrium must be reached where even resistant fractions are degraded at a rate approximating their accession.

Most probably, a section of the saprobiota develops the capacity to degrade resistant fractions. This section of the biota is probably comprised of free living microörganisms although it is conceivable that commensal or symbiotic organisms in the gut of some part of the fauna could be at least partially active in this regard. Since most soil and litter animals have a symbiotic relationship with fungi and other microörganisms, it is difficult to separate the effects of the two sections of the biota and perhaps undesirable to consider either of them in isolation (see Wallwork, 1970). For example, measurement of respiration in soil cores assesses that due to the total biota, not just that of any one section. As an index of their saprophytic activity, even soil animal respiration suffers from the drawback that particulation, increases in surface area, innoculation with the spores of microörganisms and rejuvenation of their colonies may be more significant

to breakdown than respiration *per se*. It is not disputed that fungi and bacteria with their high respiratory rates and broad spectra of enzymatic activity are ultimately responsible for most chemical breakdown but it is considered that without the activity of soil animals degradation of many substrates would be slow indeed.

BIOCIDAL CHEMICALS AND THE LITTER COMPONENT

Biocidal chemicals usually have, at least initially, a depressing effect on most taxa exposed to them. Whether this depression continues is dependent on the persistence and spectrum of toxicity of the biocide applied and the levels of tolerance of the taxa within the treated populations. The secondary outbreaks and flarebacks of agricultural pesticide practice (Ripper, 1956) have their counterparts in natural ecosystems. One well known phenomenon, illustrated in the present study, is the increased number of Collembola in mixed species populations exposed to DDT. The alteration in the balance of taxa in biocide treated populations is general and gives rise to an overall faunal disharmony where applications cover large areas and are repeated in time.

Biomass is usually reduced by biocide application and if the figures for the taxa assessed in the present study are converted to biomass using the factors provided by Edwards (1967), excluding the Araneae, a general reduction is obvious. Carbaryl induced a more marked and prolonged reduction than DDT. An exception to this statement is the

biomasses of the populations treated at the lower levels of DDT which were, on two occasions, higher than those of the control. This is mainly due to an increase in the biomass of the Collembola. In the case of both chemicals, the effect of dosage was marked and populations treated at the higher levels had consistently lower biomass.

It appears that the balance of soil animal taxa can be markedly altered in a planned way using current biocides. In contrast to Edwards et al. (1969), it is considered that, for trophic studies, effects could be demonstrated by alteration of the balance of taxa using these chemicals. Adequate assessment of results would necessarily involve more intensive sampling than would be required in the case of total or near total elimination of various faunal components.

RATIO OF LITTERFALL TO LITTER

In various publications and in discussions of litterfall, litter accumulation and breakdown, the subject of weight ratios, particularly those of litterfall to total litter weight and the ratios of the L to FH have been frequently broached. A feature of these, rarely explicit, is that these ratios give information on the rate of breakdown of the litter. For example, Forrest and Ovington (1970) state that 'the litter layer is equivalent in weight to about 5 or 6 years of litterfall'. Whether or not the intention of the authors, this could be construed to mean that the litterfall of any one year is completely broken

down 5 or 6 years later. Alternatively, the statement could mean that at any one place and time, the depth, weight, volume, etc. of litter represents 5 or 6 years fall.

The assumptions implicit in such reasoning are worth considering. Firstly, it is assumed that litterfall is the sole source of organic matter. Further assumptions include homogeneity of the input litterfall and other organic matter, linearity in the decomposition processes and stability in the mass of the forest floor.

The first assumption probably does not involve major errors since litterfall is undoubtedly the main source of organic matter and mineral element accession by the forest floor. It is, however, not the only source and the magnitudes of leachates from the canopy and aeolian deposition may be considerable, especially for inorganic elements.

Litterfall is obviously not an homogeneous substrate. The various physical fractions differ in their chemical constituents and thus their breakdown rates while woody parts especially tend to be disproportionately represented in the litter layers as compared with the input litter fall. Figures presented earlier for carbon dating of soil organic matter demonstrate the extreme resistance of certain fractions to microbial decomposition. Patently, litter layers develop with time and even after a true equilibrium is attained (if such indeed exists) they are still subject to random disturbing effects such as fire, storm, pathogens and plant parasites.

As stated above, breakdown of organic matter can be

best approximated by the sum of a series of negative exponentials. Olson (1963) also recognised the exponential nature of the decomposition process but treated litter as an homogeneous substrate.

Objections to the assumptions render the ratios of little use in assessing rate of decomposition. The level of litter accumulation after true equilibrium has been attained is probably an ecosystem constant and can perhaps be regarded as little more than a dynamically varying reservoir until more is known about litter and the nature of the parameters governing its decomposition.

SAMPLING AND DATA STRUCTURES

A major factor in a study of this nature is its considerable expense both in terms of money and the physical labour involved in collecting and processing samples. Adequate finance is an *a priori* requirement and will not be considered further here. Where statistical analysis of sample data is required considerable forethought must be applied to the requirements of the methods to be employed and data collection planned accordingly. In comparison with the physical sciences and many branches of the social sciences, collection of data in the biological sciences is often more expensive. However, it has an advantage over the former sciences in that data are potentially more complete and of better structure since the investigator has, theoretically, almost complete control over its collection.

Sample variances are frequently high since the former are often taken from heterogeneous populations. This may result from a failure to recognise the underlying heterogeneity or through a clumped distribution in the variable to be sampled. Further, variances of biological variables often alter with the magnitudes of their means due to the influences of random or cyclical phenomena such as storms, epidemics, epizootics, and seasonal growth. Skewed distributions are common in samples drawn from biological populations, especially where weights or data derived from them are involved. The rate of fall data from Chapter three represent an example of this. All of these factors militate against the use of parametric techniques but, fortunately, data may usually be transformed so that it approximately meets the requirements of these methods (Sokal and Rohlf, 1969). This is not always possible and the use of parametric statistical analytical techniques in the multivariate analysis of the litterfall data in Chapter three unfortunately necessitated deletion of the markedly heteroscedastic percentage ash data which, it was felt, would have been a source of valuable additional information in the analyses. As in the case cited above, the non-conforming variable may be analysed using a non-parametric technique although these are generally not so powerful as their parametric analogues.

Sampling intensity may be difficult to determine in many biological sampling situations and is frequently resolved in an arbitrary way. One of the major problems is temporal variation in population variance and because

of this calculation of minimum required sample size from preliminary variance estimates may be grossly in error as a result of the random disturbing influences considered above. Three interrelated main factors impinge on the selection of sample size and these are the precision desired, the variability of the population to be sampled and the cost. The acceptable relative error level is usually set prior to the study but may need to be revised in the light of high population variability. Cost is directly related to the other two factors and where this is unduly high the projected study may have to be narrowed or a lower level of relative error accepted.

Multivariate sampling poses the problem of a number of variables all with potentially different variances. Several solutions exist to this problem. The first is to ascertain the most important variables and calculate the intensity required to sample these, neglecting the remainder. Another is to take the number of sampling units required by the variable with the highest variance but to measure only a proportion of these for the less variable characters. This latter is obviously inappropriate where it is desired to use multivariate statistical analysis as all variables must be measured on each sampling unit. The final way, most often used where multivariate analysis is contemplated, is to take an arbitrary number of sampling units ensuring that adequate degrees of freedom will be available for comparison (S. John, pers. comm.).

ABSTRACT

A study was conducted on selected aspects of the nutrient cycles in a New South Wales conifer forest. The present work comprises a review of the literature pertaining to nutrient cycling in conifer forests considering the latter as examples of an open system. Results of experimental work on litterfall and the litter component of the cycles are also presented.

The experimental work is reported in three sections. The first is a comparative study of the magnitude of litterfall and chemical return in four species of Coniferae viz. Pinus lambertiana, Pinus nigra var. maritima, Pinus ponderosa and Pseudotsuga menziesii. Weights of organic matter as its leafy, woody, male and female reproductive components were assessed for each sample. Chemical analysis of litterfall for nitrogen, phosphorus , potassium, calcium, magnesium, iron, manganese and zinc yielded data on the concentrations of these elements and their total weights accessed over each sample interval in litterfall. Univariate and multivariate analyses of the significance of the differences between species within collection intervals and within species over all collection intervals were made for both the concentration and weight of fall data. The latter data were converted to rates of fall to allow the comparison of unequal sample intervals.

The remaining portion of the first section is a study of the spatial pattern of the accession of litterfall as

its leafy and woody components and also of the concentrations and weights of the elements listed above. These variables were related to the distances of the nearest four trees from the individual sampling points and their sizes as measured by diameter at breast height over bark. Statistical techniques used included multiple regresseion and canonical correlation analyses.

The second section is a study of the litter component of the P. nigra var. maritima stand. Here, sampling was conducted with the aim of assessing the magnitude and temporal variation of the pool of organic matter and its contained mineral elements. Results are compared with those obtained from sampling the litter layers of several other conifer species growing in the same locality.

The fauna of the soil and the forest floor has a considerable influence on the breakdown of litter and its incorporation into the mineral soil. The third section comprises the results of faunal investigations in the P. nigra var. maritima stand used for the previous studies. This study was designed to assess the litter fauna present and the reactions of selected taxa to the application of two biocides (DDT and carbaryl) each applied at two dosages. Again, univariate and multivariate analyses were effected to assess the significance of the differences between treatments at each sample interval and also within treatments over all sample intervals.

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Considerable advice on the statistical analysis of results was provided by Dr. S. John, of the Department of Statistics, School of General Studies, and Professor P.A.P. Moran, of the Department of Statistics, Institute of Advanced Studies. Assistance with computation was given by the staff of the Computer Centre and I should particularly like to acknowledge the assistance of Dr. D.M. Ryan and Mr. I.R. Simpson.

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